THE ECOLOGICAL IMPORTANCE OF *ARTIBEUS* AND OTHER FRUGIVOROUS BATS WITHIN THE IWOKRAMA FOREST IN GUYANA, SOUTH AMERICA: AN INVENTORY OF DISPERSED SEEDS

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Abstract:

Artibeus species are primarily frugivores, and through the ingestion and defecation of consumed fruits, they play a critical role in their environment through the dispersal of early successional and pioneer species contributing to reforestation of fragmented habitat. The objective of this study was to survey the plant species dispersed by all captured frugivorous bats with special emphasis on the ecological contribution of *Artibeus obscurus, A. planirostris,* and *A. lituratus* within the Iwokrama Forest in Guyana. Research was conducted in concordance with long-term vertebrate monitoring conducted during the summer rainy season by Operation Wallacea since 2011 within the Iwokrama and Surama Forests. In summer of 2013, stomach contents were taken from collected frugivorous bats, and fecal samples were taken from all captured frugivorous bats. Samples were used for comparative analysis among sympatric frugivorous bat species. *Artibeus lituratus, A. planirostris,* and *A. obscurus* accounted for an average of 44% of total captures and 65% of total captured frugivores. Twenty plant species were identified in fecal samples, including *Cecropia latiloba*, a species previously unknown to be bat dispersed. *C. latiloba* was dispersed most commonly by *A. planirostris* and *A. obscurus*. Twenty-three of 63 total fecal/stomach content samples (37%) represent new dispersal records. These results further our understanding of seed dispersal by Neotropical bats.

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Introduction.

Within Guyana, bats represent over 51% of mammalian species (Voss and Emmons 1996). The rainforest of the Iwokrama reserve in Guyana, South America, is home to over 86 species of bats (Lim and Engstrom 2001a). This is one of the highest bat species diversity records recorded for any protected area in the world. Phyllostomidae, or the New World "leaf-nosed" bats, is the most diverse family in the Neotropics. There are six subfamilies, 44 genera, and over 143 species of phyllostomid bats (Gardner 2007). This single family accounts for over 50% of Guyanese bat diversity (Voss and Emmons 1996). Stenodermatinae is the most diverse subfamily of phyllostomids, with 14 genera and over 60 South American species. Species within this subfamily are either predominantly or entirely frugivorous (Mello et al. 2011); their characteristics include a short, round face and the absence of a tail (Gardner 2007).

The genus *Artibeus* belongs to the subfamily Stemodermatinae and is composed of 22 species overall, and 14 species known to South America (Gardner 2007). Coloration is generally pale to dark brown with a typically pale venter and darker dorsum. Most have facial stripes of varying definition and lack dorsal striping. These bats are characterized by medium-sized ears and a short, broad skull. Inner upper incisors are distinctly larger than outer incisors and appear bilobed (Marques-Aguiar 2007). The genus *Artibeus* has been considered a monophyletic group. However, recent molecular studies have suggested that *Artibeus* is paraphyletic, adding two subgenera (Straney et al. 1979, Wetterer et al. 2000). The smaller species were placed in subgenus *Dermanura* and *A. concolor* was placed in subgenus *Koopmania*, leaving the larger species in subgenus *Artibeus* (Wetterer et al. 2000).

Artibeus lituratus, the great Artibeus, is geographically distributed from Mexico south to southern Brazil, northern Argentina, Bolivia, and Trinidad and Tobago (Simmons 2005, Marques-Aguiar 2007). These bats are found primarily in lower elevations near riparian areas, evergreen forests, dry uplands, and less frequently in deciduous, thorn, and cloud forest (Handley 1976). It is the largest of the Neotropical fruit bats with a forearm length of 64-76 mm and a weight of 44-87 grams (Nowak 1994). It has light brown fur and very distinct bright white supraorbital stripes (Simmons and Voss 1998). This species is known to forage high in the canopy, and roosts in caves and palm trees in colonies of upwards of 25 individuals (Handley 1976). Colonies consist of a single male and a harem of usually 2 to 14 females (Munoz-Romo et al. 2007). This species is known to have a greater home range than either *A. planirostris* or *A. obscurus*. Fleming et al. (1972) suggested that home range size is proportional to body size.

Artibeus planirostris, Spix's Artibeus, is distributed from northern Argentina through Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Venezuela, and Suriname (Marques-Aguiar 2007). Recent phylogenetic evidence supports the recognition of this species as separate from *A. jamaicensis* (Lim et al. 2004, Larsen et al. 2007). This species is found primarily in lowland tropical rainforest (Hollis 2005). It has ashy brown fur with lighter shoulders, less pronounced facial striping than *A. lituratus*, and frosted ventral fur (Simmons and Voss 1998). The forearm measures around 66 mm (Hollis 2005). Like *A. lituratus*, this species is a large canopy frugivore, seeking out open habitats of the upper canopy and ultilizing creek corridors and treefall gaps (Charles-Dominque and Cockle 2001). However, *A. planirostris* has also been known to opportunistically utilize the forest understory (Bernard 2001). Additionally, like *A. lituratus*, this species is known to roost in

tree hollows and foliage, and forms groups of a single adult male with up to 14 adult females in a harem (Morrison and Handley 1991).

Artibeus obscurus, the black Artibeus, is distributed east of the Andes in southern Colombia and Venezuela, eastern Ecuador, Peru, Bolivia, most of Brazil, and into the Guyanas (Marques-Aguiar 2007). It is found primarily in tropical humid mainland forests, but has also been found in savannah regions (Bernard and Fenton 2002, Faria 2006). This species has a much darker coloration, less pronounced facial striping, and longer, softer fur than either *A. lituratus* or *A. planirostris* (Simmons and Voss 1998). Forearm measurements range from 56-63mm (Lim and Engstrom 2001a). *A. obscurus* is considered a canopy frugivore as well as an opportunistic forager (Bernard 2001). Contrary to the previously described species, *A. obscurus* has a smaller home range and utilizes a greater variety of habitats, such as edge habitat and high forest understory (Delaval et al. 2005). Additionally, this species forages earlier in the evening than either *A. lituratus* or *A. planirostris* (Delaval et al. 2005). Past Operation Wallacea (Opwall) surveys in Iwokrama have consistently found these three species of *Artibeus* in disproportionately high abundance and in relative equilibrium when compared to other captured species (Lim and Engstrom 2001b, Bicknell et al. 2011, 2012).

Species of stenodermatines are nearly exclusive frugivores, as they have a significant or complete dependence on fruit for a living (Mello et al. 2011). Most phyllostomids will rotate among five plant genera *Cecropia, Ficus, Piper, Solanum*, and *Vismia* based on seasonal availability (Fleming 1986). These bats are critical in the dispersal of these genera as well as the maintenance of floral composition and distribution (Bonaccorso and Gush 1987). This is true not only of endozoochory through ingestion and dispersal of their

preferred plant genera, but also epizoochory through the dispersal of large-seeded plants (Melo et al. 2009). At times when their preferred food sources are unavailable or when nutritional supplement is needed, stenodermatine species will consume insects, leaves, pollen, nectar, flower parts, and have been known to visit mineral licks (Gardner 1977, Bravo et al. 2012). The frequency and extent to which bats will change among food items depends on the abundance of their preferred food resources and competitors; therefore, this varies temporally and geographically among species (Humphrey and Bonaccorso 1979).

Provided that phyllostomids commonly forage on five core plant genera, dietary overlap and competition among bat species would be suspected. However, several studies have found resource partitioning among Neotropical frugivorous bat species with little dietary overlap (Muller and Reis 1993, Hernandez-Conrique et al. 1997, Lopez and Vaughan 2007). Characteristics such as foraging strata, dietary preferences, craniodental morphology, and body size appear to permit coexistence and partitioning among sympatric genera (Freeman 1988, Charles-Dominique and Cockle 2001). Fleming (1986) describes a close association between phyllostomid genera (*Artibeus*, *Carollia* and *Sturnira*) and particular plant genera in Costa Rica. *Artibeus* species foraged predominantly on *Ficus* and *Cecropia*. *Carollia* prefed to feed on the plant genus *Piper*, and *Sturnira* were selective toward the plant genus *Solanum*. Lopez and Vaughan (2007) found that five of the six most commonly caught sympatric frugivorous bats in Costa Rica had a diet that was composed of predominately one or two species of plant, providing further support for partitioning among genera.

Over 80% of plant species in the Neotropics rely on frugivorous vertebrates for the dispersal of their diaspores (effective dispersal unit) (Howe and Smallwood 1982). Geiselman et al. (2002 onward) has reported a total of 549 species in 191 genera forming 62

plant families that are dispersed specifically by bats. As a large number of plant species dispersed by Neotropical phyllostomids are pioneer species, contributing to forest regeneration, Presley et al. (2009) have suggested that they could represent a keystone taxon (Muscarella and Fleming 2007). A keystone taxon or species can be defined as one of a limited number of taxa or organisms contributing disproportionately to the critical processes necessary for ecosystem functioning (Folke et al. 1996). Given their dietary preferences, dispersal capacity, and high quality of dispersal, *Artibeus* species likely fit this definition.

In many cases, bats are the sole or primary dispersal agents and pollinators for numerous tropical plants (Fleming and Heithaus 1981, Fleming 1988, Galindo-Gonzalez et al. 2000). They are set apart as proficient dispersal agents by the "quality" with which they disperse diaspores (Humphrey and Bonaccorso 1979). In this sense, quality refers to diaspores remaining relatively undamaged, dispersal of diaspores over fair distances, and diaspores being dropped in a suitable environment for germination (Lobova et al. 2009, Presley et al. 2009). Additionally, fruits commonly foraged by *Artibeus* are generally nutritionally poor, which requires the consumption of a large amount of fruit pulp each night to meet their dietary needs (Fleming 1986). *Artibeus* species usually make between 30 and 40 foraging bouts per night, processing up to two times their own bodyweight in fruit (Charles-Dominique and Cockle 2001). Between foraging bouts, these bats carry fruit to feeding roosts where they ingest pulp and drop boluses consisting of indigestible material (Nowak 1994). This results in a single bat dispersing hundreds and up to thousands of diaspores each night, further contributing to their quality of dispersal.

There are several factors that suggest that *Artibeus* species play a disproportionate role within the ecosystem of the Iwokrama forest. Due to their overwhelming abundance and

integral role as primary dispersal agents, *Artibeus* could contribute heavily to the overall function of the network. The objective of this study was to survey the plant species dispersed by all captured frugivorous bats with special emphasis on the ecological contribution of *Artibeus obscurus, A. planirostris,* and *A. lituratus* within the Iwokrama Forest in Guyana. I hypothesized that *Artibeus* diet was composed of primarily early successional and pioneer species, and when compared to other frugivores, their most commonly foraged species will be relatively unique. Furthermore, I hypothesized that bat/plant genus associations in Guyana will be consistent with the observations of Fleming (1986). A secondary objective of this study was to describe the local bat community through analysis of mist net survey data, focusing on species richness and capture rates at five sites within Iwokrama. As far as is known, this is the first study of frugivorous bat diet conducted in Guyana.

Methods:

Study site

The Iwokrama reserve is composed of 371,000 ha of pristine rainforest located in central Guyana in the Potaro-Siparuni Region (Figure 1). Iwokrama was set aside by the government of Guyana in 1990 under the auspices of the Commonwealth Secretariat (Lim and Engstrom 2001a). It is divided into two approximately equal parts: half is strictly a wilderness reserve set aside for the study of biodiversity, whereas the other area is for research in harvest of rainforest resources (Bicknell et al. 2012). It is bordered on the east by the Essequibo River, on the north by the Siparuni River, on the west by the Takutu, Sipariparu, Burro-Burro, and Surama Rivers, and on the south by the Kuiparu River and Lady Smith Creek. A 70km road passes through the center of the reserve (Lim and Engstrom 2001a). The Surama Forest is located just outside Iwokrama, bordering the southwest corner.

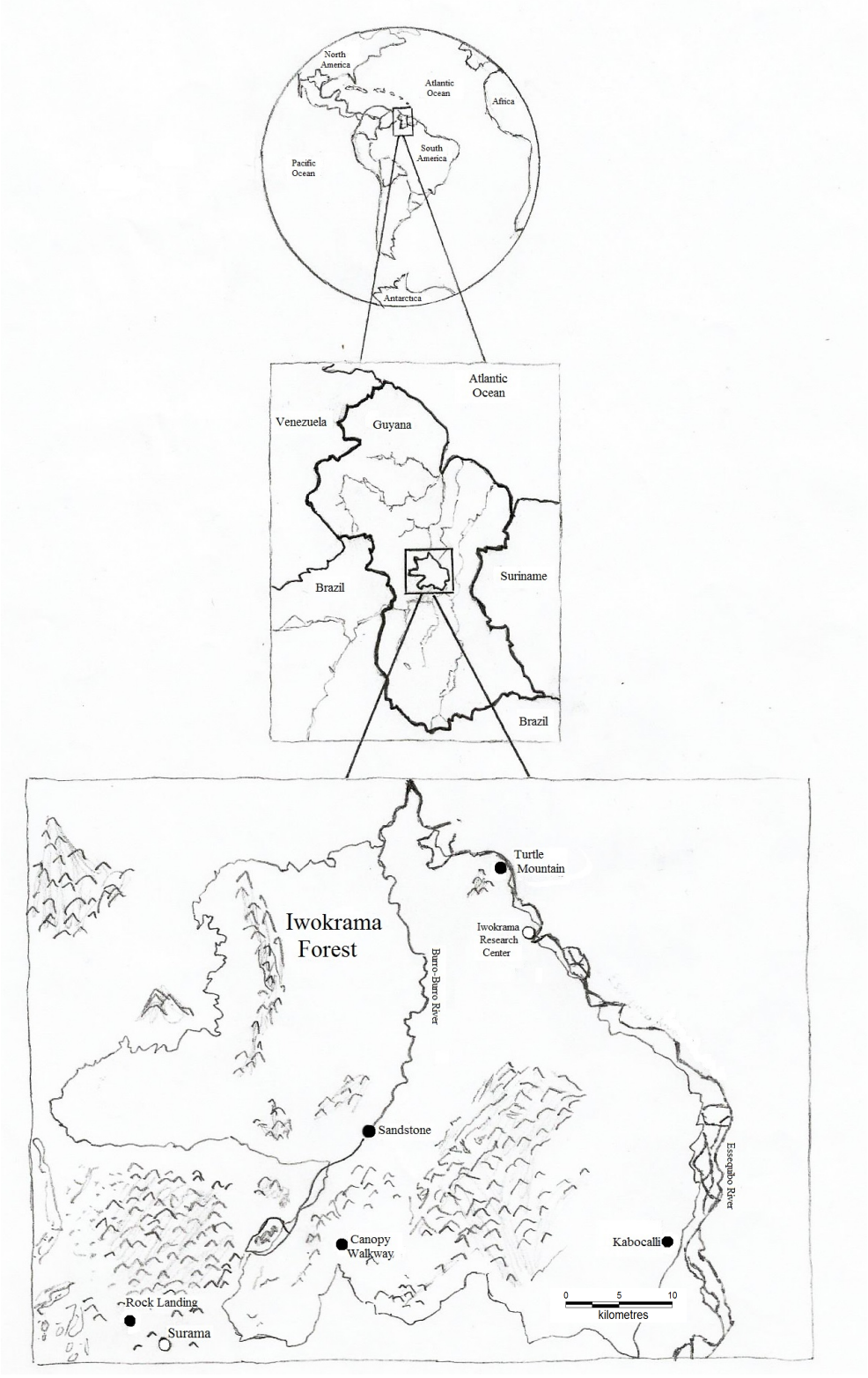

FIGURE 1. Map of the Iwokrama Forest highlighting survey sites (black dots) and other sites of importance (white dots).

In the summer of 2011, Opwall initiated a long-term vertebrate monitoring project within the Iwokrama and Surama Forests. Opwall is an organization consisting of a network of academics from North American and European universities who design and implement biodiversity and conservation management programs at field sites in 11 countries around the world, including Iwokrama. Partnerships are formed with organizations in host countries, which receive high quality long-term biodiversity data in exchange for providing study sites and other services for Opwall expeditions. Opwall is entirely funded by students seeking to participate in summer field expeditions.

Since 2011, five sites in this region have been surveyed for bats (Bicknell et al. 2012). Four sites, Turtle Mountain (N4.73186° W-58.71775°), Kabocalli (N4.28784° W-58.50848°), Canopy Walkway (N4.24963° W-58.90933°) and Sandstone (N4.38388° W-58.92127°), are located within Iwokrama; and a fifth site, Rock Landing (N4.17972° W-59.08286°), is within the Surama Forest (Figure 1). The reserve is characterized by low-lying terra firme tropical rainforest dominated by *Chlorocardium rodiei*, *Eperua falcata*, *Dicorynia guianensis*, *Mora excelsa* and *Swartzia leiocalycina* (Bicknell et al. 2011). Average annual rainfall for the region is approximately 3000 mm yr, 400-500 mm during rainy season months (April to July) and 200 mm during most other months. Temperatures range from an average low of 22°C at night during the July wet season to an average high of 36°C during the October dry season (Hammond 2005a, Bicknell et al. 2011).

Sampling strategy

Bat surveys were conducted in the Iwokrama and Surama Forests during the summer wet-season from late June through mid August (20 June to 18 July in 2011, 2 July to 12 August in 2012, and 16 July to 12 August in 2013). Sites were surveyed using 18 understory

mist nets arranged in a 100 m grid comprised of three transects branching off one of the large mammal transects used in other Opwall surveys. Six, 12 m nets were positioned in "T's" separated by 50 m along each of the three transects (Figure 2). Nets were placed in the same locations year to year, unless otherwise precluded by fallen trees. Surveying methods remained consistent each year in order to make accurate long-term assessments of biodiversity and species abundance. Nets were opened at 18:00 h and closed at 00:00 h. In the event of ongoing heavy rain, nets were closed in an effort to prevent captures during periods when the nets were not checked, as prolonged exposure to lower temperatures when combined with exhaustion could prove fatal for smaller species of bats captured in nets. Furthermore, bats typically do not fly during heavy rainfall (Voigt et al. 2011). Captured individuals were weighed, sexed, aged, and marked for recapture with a 1 mm wing puncture and released (20, 6, and 3 recaptures in 2011, 2012, and 2013 respectively) (Brunet-Rossinni and Wilkinson 2009, Bicknell et al. 2012). Species were identified using keys developed by Lim and Engstrom (2001a). Only three of the five sites were surveyed in all three years. Canopy Walkway was surveyed for only two years, due to logistical limitations, and the 2011 Rock Landing survey was conducted using methods that differed from the following years. Therefore, these sites (Canopy Walkway and Rock Landing) were analyzed independently.

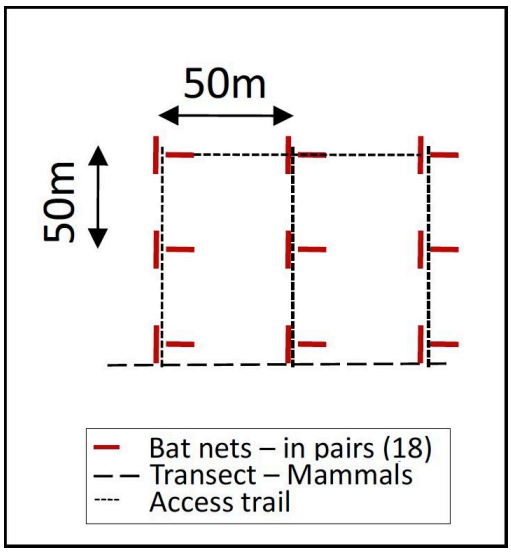

FIGURE 2. Mist net (12m) array used to survey for bats in Iwokrama in summer 2011-2013 (from Bicknell et al. 2012).

In 2013, fecal samples were collected from captured frugivores. Bats were held in canvas capture bags for no longer than two hours to allow time for captured individuals to defecate in order to maximize sample yield (Lopez and Vaughan 2004). Canvas bags were cleaned of remnant feces between captures to prevent cross contamination of fecal samples. Bats were released after collection of morphometric data and a fecal sample, if provided. In 2012 and 2013, voucher specimens were collected of one individual per species per night of surveying (Appendix 1). All procedures were consistent with recommendations for handling wild taxa (Sikes et al. 2012), and all procedures followed taxon-specific guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and the Institutional Animal Care and Use Committee at Angelo State University (IACUC Approval Number 1312). Specimens were deposited at the Angelo State Natural History Collection, in San Angelo, Texas, and the Royal Ontario Museum in Toronto, Ontario. Specimens were used to confirm species identification. Stomach contents were taken from collected frugivorous individuals

for later dietary analysis. Samples were stored in two-milliliter screw-cap microcentrifuge tubes filled with 70% ethanol (Aguirre et al. 2003). Stomach content samples were not collected from individuals who had provided an earlier fecal sample.

In 2013, fallen fruit and any fruit available on plants surrounding the bat net and large mammal transects at each site, in addition to available accompanying plant parts, were collected and stored in Whirl-pak™ bags containing 70% ethanol (Lopez and Vaughan 2007). Furthermore, in 2012 and 2013, any fruit carried into the nets by bats was documented and collected, and the species of bat carrying the fruit was recorded. All collected fruit and fecal samples were identified, and the contained diaspores were dried in order to build a reference collection. Diaspores from collected fecal samples and stomach contents were sorted, separating each type found within a sample, and tentatively identified using images and morphological characteristics as described by Lobova et al. (2009). Diaspore identifications were later confirmed using the reference collection of Dr. Tatyana Lobova at Old Dominion University in Norfolk, Virginia. The number of types, number of diaspores of each type, and morphometric data of each type were recorded for each collected sample. Additionally, all diaspore types were photographed for digital documentation.

Data Analysis

Bat and plant genus associations were tested using a permutation test for independence (Chihara and Hesterberg 2011) using a chi-square test function in the coin package in R (Hothorn et al. 2006, 2008). Annual capture rates were compared using a test of equal or given proportions in R (Newcombe 1998). For comparisons across the three years, the Holm P-value adjustment method was applied using the p.adjust method in R to account for elevated type I error due to multiple comparisons (Wright 1992). Additionally,

comparisons of proportion of net hours lost due to rainfall (PNHL) from year to year were calculated in this way.

PNHL was calculated in order to gauge the effect of rainfall on survey effort between and among sites year to year. PNHL is calculated by taking the difference between the maximum potential number of net hours and the actual number of net hours for a given site, and dividing this number by the maximum potential net hours. Maximum number of net hours (nh) was quantified by multiplying the number of nets at each site (18 nets) by the maximum number of hours the nets could be open per night (6 hours), and multiplying this number by the number of nights each site was surveyed. PNHL was calculated by dividing the net hours lost due to rain by the maximum number of net hours possible. In addition to rainfall, a portion of maximum potential survey effort was lost due to missing nets. This contributed minimally to loss of survey effort, and resulted primarily from a later than expected arrival to a site, restricting our ability to put up all 18 nets in the grid. In 2011, Sandstone was missing one net for one night. In 2012, Turtle Mountain was missing one net for one night, and Canopy Walkway was missing eight nets for one night. In 2013, no survey effort was lost due to missing nets. For these instances, the number of net hours lost due to missing nets was added to the actual net hours in order to isolate net hours missing due to rainfall. PNHL is only a relative measure of rainfall as net closure was subjectively established based on how heavy the rain was falling.

Results:

Diet Analysis Results

Overall, 75 fecal samples and 39 stomach content samples were collected during the summer 2013 season from 114 individuals of 14 bat species. Collectively, 63 of the combined 114-fecal/stomach content samples contained diaspores. The remaining 51 samples contained a combination of fruit pulp, plant material, and some insect matieral. Additionally, five fruits were collected from bats that had flown into the nets in 2012, and four fruits were collected in 2013 (Table 1). Of the 63 samples containing diaspores, *Artibeus lituratus, A. planirostris,* and *A. obscurus* accounted for 27 samples; *Carollia perspicillata* accounted for 25 samples; and other bat species (*Artibeus gnomus, Phyllostomus hastatus, Platyrrhinus helleri, Rhinophylla pumilio, Sturnira lilium, Sturnira tildae,* and *Vampyressa bidens*) represented 11 samples. Overall, 20 plant species were identified in collected samples, including *Cecropia latiloba*, a species previously unknown to be bat dispersed (Figure 4, Appendix 3) (Lobova et al. 2009). *Cecropia latiloba* was dispersed most commonly by *Artibeus planirostris* (three samples) and *A. obscurus* (two samples). However, a single dispersal record was also observed for *A. lituratus*, *C. perspicillata, P. helleri*, and *V. bidens.*

The apparent "seeds" of *Cecropia* species are actually individual fruits ingested by bats from an infructescence. Thus, it is the fruit of *Cecropia* that serves as the diaspore for these species (Lobova et al. 2003). Characteristics useful in distinguishing the fruit of the three collected species of *Cecropia* include shape, size, color, and surface appearance (Figure 3). Fruit of *Cecropia obtusa* are lanceolate to ellipsoid in shape, with one or both ends appearing more or less acute, and are approximately 2.9 x 0.8 x 0.8mm in size. Their surface appears indistinctly undulate to rugose, and is brown in color, with a glossy appearance.

Fruit of *Cecropia sciadophylla* are ellipsoid in shape, with one or both ends acute, and are approximately 2.9 x 1.2 x 0.9 mm in size. Their surface bears distinct tubercles, which are smaller or absent at the ends of the fruit. They are dark brown in color and appear glossy (Lobova el al. 2003). Based on observations from the current study, fruit of *Cecropia latiloba* are broadly lanceolate to broadly ellipsoid in shape, with ends obtuse to acute, and are approximately 2.7 x 1.1 x 0.9 mm in size. Their surface appears tuberculate to rugose, and is brown to dark brown in color, with a glossy appearance.

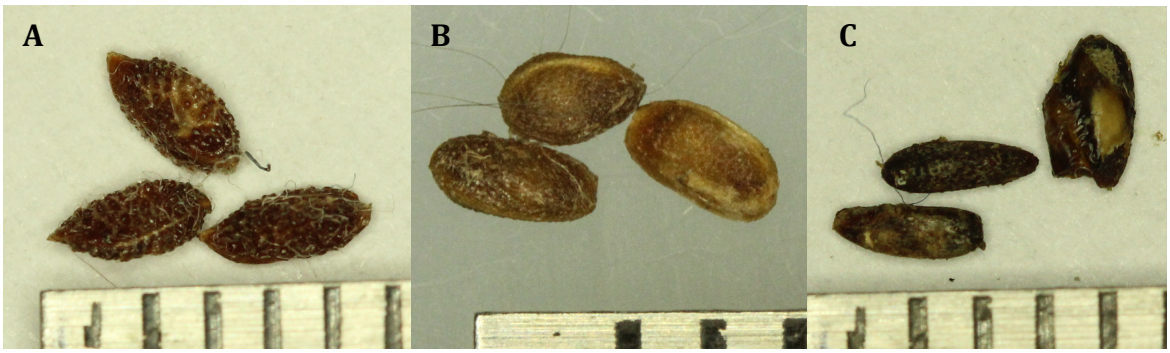

FIGURE 3. Images showing diaspores of *Cecropia sciadophylla* (A), *Cecropia latiloba* (B), and *Cecropia obtusa* (C). Diaspores were isolated from the following collected fecal samples: *C. sciadophylla – Artibeus lituratus*; *C. latiloba – Artibeus obscurus*; and *C. obtusa – Artibeus obscurus*. Samples collected July-August 2013 from the Iwokrama Forest, Guyana. Scales in images in millimeters.

Additionally, seven records of known bat-dispersed plant species being dispersed by new bat species were found (Lobova et al. 2009) (Table 2). When considering bat/plant genus associations, there was a significant association between *Artibeus* and *Ficus/Cecropia* and *Carollia* and *Piper/Solanum* (χ^2= 42.1, df= 3, p<0.001) (Figure 4). Low sample sizes precluded statistical analysis of other genera. Calculations of dietary overlap among bat species were not possible due to low fecal/stomach content sample size. The majority of

collected samples were from *Artibeus* and *Carollia*, which contained two overlapping plant species, each with only a single dispersal record in the opposing genera. There were not enough samples to compare other genera.

Fecal sample data for Turtle Mountain show a high abundance of *Ficus* and *Cecropia*, with seven *Ficus*-containing samples of a single species (*F. nymphaeifolia*) and ten *Cecropia*-containing samples of three species (*C. latiloba*, *C. sciadophylla*, and *Cecropia* sp.). There were three additional samples, containing *Anthurium trinerve, Philodendron* sp., and *Piper bartlingianum*, and two fecal samples that did not contain diaspores. Kabocalli had five samples of three plant species, the lowest number of collected samples of any site. *Ficus panurensis* was the most common species with three records, followed by *Piper anonifolium* and *Senna quinquangulata* with a single record each. There were 23 fecal samples collected from Sandstone, 14 of which contained diaspores. The remaining nine samples contained a combination of fruit pulp, plant material, and some insect material. Two of the 14 diaspore-containing samples were from *Artibeus obscurus*, 8 were from *Carollia perspicillata*, 3 were from *Sturnira tildae*, and one was from *Rhinophylla pumilio.* Of the 12 samples collected from the smaller frugivores, 11 contained *Piper* sp., one contained a *Paulinia* sp., and 1 contained a *Philodendron* sp. The two *Artibeus* samples each contained *Cecropia latiloba*. Sandstone was the only site in which fecal samples did not contain *Ficus* species. By far the most abundant plant species collected was *Piper bartlingianum* with 10 records. This species was most commonly dispersed by *Carollia perspicillata* (6), followed by *Sturnira tildae* (3) and *Rhinophylla pumilio* (1). Rock Landing had the highest diversity of plant species collected from the greatest number of diaspore-containing samples; 10 species of plants were collected from 21 samples. Furthermore, this site had the highest number of *Ficus* species

collected and the highest number of *Ficus*-containing samples (eight samples of four species: *Ficus insipida, F. panurensis, F. maxima, F. nymphaeifolia*) and was second to Turtle Mountain for number of samples containing *Cecropia* (five samples of two species: *Cecropia latiloba, C. sciadophylla*). Of the 13 combined *Ficus* and *Cecropia* samples, ten were dispersed by *Artibeus*. *Carollia perspicillata* was responsible for dispersing the remaining four plant species collected at this site: *Vismia cayennensis, Senna quinquangulata, Piper trichoneuron,* and *Rollinia exsucca*.

TABLE 1. Fruit collected after being dropped in mist nets in the Iwokrama Forest, Guyana from late June to mid August in 2012 and 2013.

Plant Species	**Bat Species**	**Year Collected**
Ficus sp. 01	*Artibeus obscurus*	2012
Ficus sp. 02	*Artibeus planirostris*	2012
Chrysobalanaceae sp. 01	*Artibeus obscurus*	2012
Chrysobalanaceae sp. 01	*Artibeus obscurus*	2012
Chrysobalanaceae sp. 01	*Artibeus planirostris*	2012
Chrysobalanaceae sp. 02	*Artibeus obscurus*	2013
Chrysobalanaceae sp. 03	*Artibeus lituratus*	2013
Ficus maxima	*Artibeus planirostris*	2013
Piper bartlingianum	*Carollia perspicillata*	2013

TABLE 2. New records of plant species documented in fecal samples of bat species acting as dispersal agents in the Iwokrama Forest, Guyana from late June to mid August in 2012 and 2013.

Bat Species	**Plant Species (# Individual Samples)**
Artibeus gnomus	*Ficus panurensis*
Artibeus lituratus	*Cecropia latiloba*
Artibeus obscurus	*Cecropia latiloba* (2)
	Ficus maxima
Artibeus planirostris	*Cecropia latiloba* (3)
	Ficus panurensis (3)
Carollia perspicillata	*Cecropia latiloba*
	Paullinia sp.
	Philodendron guianense
Platyrrhinus helleri	*Cecropia latiloba*
Sturnira lilium	*Cecropia sciadophylla*
Vampyressa bidens	*Cecropia latiloba*
	Ficus nymphaeifolia (2)

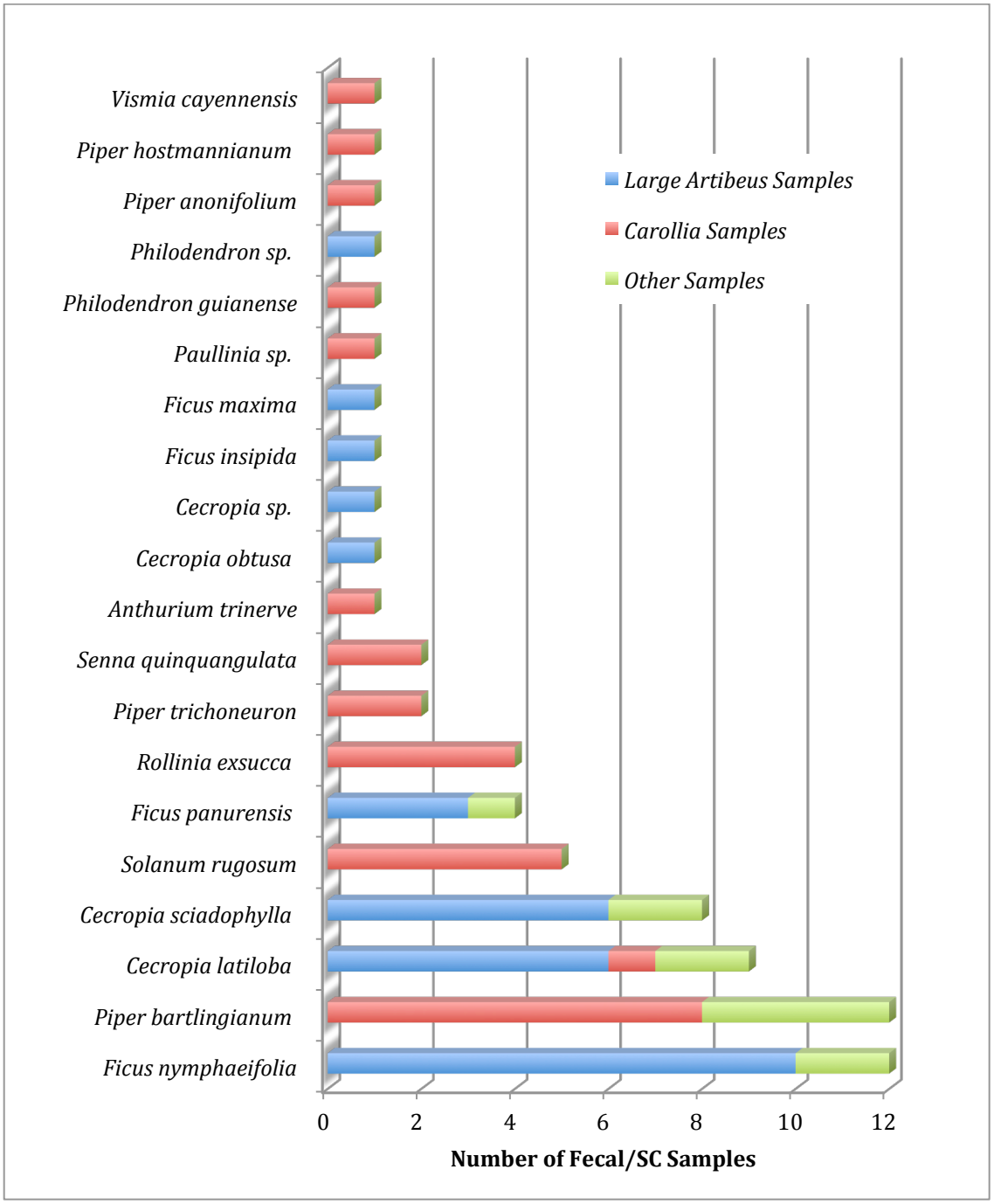

FIGURE 4. Plant species identified in collected fecal and stomach content (SC) samples, and the number of samples in which each plant species occurred from *Artibeus* (blue), *Carollia* (red), or other bat genera (*Rhinophylla*, *Phyllostomus, Platyrrhinus*, *Sturnira, Vampyressa,* and non-focal *Artibeus*). Non-focal *Artibeus* species are represented by a single sample collected from *Artibeus gnomus*, a smaller *Artibeus* species within the subgenus *Dermanura* (Simmons 2005). Samples collected July-August 2013 from the Iwokrama Forest, Guyana.

Bat Survey Results

Over the course of three seasons I accumulated 6,137 net hours (actual) of survey effort among the five sites (Figure 5a), and captured 731 individuals of 38 species (Table 3, Appendix 2). Capture rates ranged from a high of 0.262 captures/nh at Rock Landing in 2013 to a low of 0.048 captures/nh at Canopy Walkway in 2012 (Figure 6). The five most commonly captured species were *Artibeus planirostris* (186), *A. obscurus* (87), *A. lituratus* (85), *Carollia perspicillata* (78), and *Lophostoma silvicolum* (58). Eight species were captured only once: *Carollia brevicauda, Cormura brevirostris, Lophostoma brasiliense, Micronycteris brachyotis, Saccopteryx bilineata, Sturnira lilium, Thyroptera tricolor,* and *Vampyrum spectrum.* Opwall surveys have added two previously unrecorded species to the list of species known to occur in Iwokrama, *Mimon bennettii* and *Furipterus horrens*. This brings the total number of recorded species from 86 to 88 (Lim and Engstrom 2001a).

When comparing the species richness of each site (Figure 5b), on average Sandstone and Rock Landing had the highest richness with 15 species, followed by Kabocalli (14.3), Turtle Mountain (14), and Canopy Walkway (9.5). When considering individual sites/seasons, Turtle Mountain had both the highest species richness of any site (20 species in 2011) and the lowest species richness of any site (7 species in 2012). Turtle Mountain also had the largest fluctuation in survey effort from year to year, with a decrease of 381 net hours from 2011 to 2012, followed by Canopy Walkway with a decrease of 302 net hours from 2011 to 2012 (Figure 5a).

When considering the combined Turtle Mountain, Kabocalli, and Sandstone data from 2011 to 2012, the number of individuals decreased by 40%, the number of species decreased by 33%, and the capture rate fell by 45% (Figure 5 and 6). From 2012 to 2013,

there was a slight resurgence, with the number of captured individuals increasing by 23%, the number of species increasing by 10%, and the capture rate increasing by 38%. Differences among capture rates each year were significant (χ^2= 41.15, df= 2, p< 0.02). Fluctuation in the number of captured individuals, number of species, and capture rates for Canopy Walkway and Rock Landing match this trend. The only site that differs from the overall trend is Kabocalli, where these variables significantly declined from year to year (χ^2= 57.6, df= 2, p< 0.03). Furthermore, Kabocalli was the only site to have a decrease in capture rate from 2012-2013.

Fluctuation in *Artibeus* capture rates (combined number of captures of *Artibeus lituratus, A. planirostris,* and *A. obscurus* divided by the actual net hours for each site) from year to year for all sites match the observed trend seen in the combined Turtle Mountain, Kabocalli, and Sandstone dataset. Fluctuation in *Artibeus* captures rates between 2011-2012 and between 2011 and 2013 was significant (χ^2= 31.3, df= 2, p< 0.001). However, the increase from 2012-2013 was not significant (χ^2= 31.3, df= 2, p= 0.664). The only site to deviate from this trend was Sandstone, were there was no significant fluctuation in *Artibeus* capture rates from year to year (χ^2= 3.26, df= 2, p= 0.196). Furthermore, *Artibeus* capture rates for Sandstone were the lowest each year of any site. *Artibeus lituratus, A. planirostris,* and *A. obscurus* (combined captures) make up a large proportion of overall total captures and proportion of total captured frugivores at each site for each year (Figure 7). The lowest values for these measurements occurred at Sandstone in 2013, where the large *Artibeus* species accounted for 18% of total captures and 25% of total captured frugivores. Interestingly, no individuals of the large *Artibeus* species were captured at Turtle Mountain in 2012. Rock Landing and Canopy Walkway were not surveyed each year, and thus appear

to have zero *Artibeus* captures in Figure 7; but at Turtle Mountain, despite catching 14 individuals, none of them were *Artibeus*.

PNHL was calculated as an indirect measure of rainfall each year. When considering PNHL for the combined Turtle Mountain, Kabocalli, Sandstone dataset, there was a significant increase from 2011 to 2012 and a significant reduction from 2012 to 2013 (χ^2= 64, df= 2, p< 0.001). The PNHL did not significant differer between 2011 and 2013 (χ^2= 31.3, df= 2, p= 0.11) (Figure 6). There was an inverse relationship between capture rates and proportion of net hours lost due to rainfall at most sites. This was most evident in the combined dataset in which years with the higher capture rates (2011 and 2013) saw a reduced PNHL, and the year with the highest PNHL saw a reduced capture rate. Two sites differ from this trend: Kabocalli and Sandstone. At Kabocalli in 2011, the capture rate was higher, despite a high PNHL; and in 2012 and 2013 both the capture rate and PNHL fall from year to year. At Sandstone from 2011 to 2012, we observed a reduction in both the capture rate and PNHL. However, from 2012 to 2013 at this site, we see the expected inverse relationship between these variables.

TABLE 3. Summary of total individuals of each species captured each year in the Iwokrama Forest, Guyana from late June to mid August in 2011-2013.

Species	2011	2012	2013
Artibeus concolor	1	0	1
Artibeus gnomus	0	2	2
Artibeus lituratus	40	15	30
Artibeus obscurus	24	32	31
Artibeus planirostris	81	35	70
Carollia brevicauda	0	0	1
Carollia perspicillata	29	18	31
Chiroderma villosum	3	0	1
Chrotopterus auritus	1	3	0
Cormura brevirostris	0	1	0
Desmodus rotundus	6	5	5
Furipterus horrens	1	0	1
Glossophaga soricina	6	10	2
Lionycteris spurrelli	0	3	2
Lonchophylla thomasi	10	11	6
Lophastoma schulzi	1	1	2
Lophostoma brasiliense	1	0	0
Lophostoma silvicolum	26	23	9
Mesophylla macconnelli	1	1	1
Micronycteris brachyotis	1	0	0
Micronycteris megalotis	3	2	0
Micronycteris minuta	1	0	0
Mimon bennettii	3	0	1
Mimon crenulatum	4	2	1
Phylloderma stenops	2	2	0
Phyllostomus elongatus	12	5	7
Platyrrhinus helleri	1	1	0
Pteronotus parnellii	11	12	10
Rhinophylla pumilio	11	4	15
Saccopteryx bilineata	0	1	0
Sturnira lilium	0	0	1
Sturnira tildae	0	0	6
Thyroptera tricolor	0	0	1
Tonatia saurophila	2	3	0
Trachops cirrhosus	5	3	2
Uroderma bilobatum	2	0	0
Vampyressa bidens	5	0	2
Vampyrum spectrum	1	0	0
Total	295	195	241

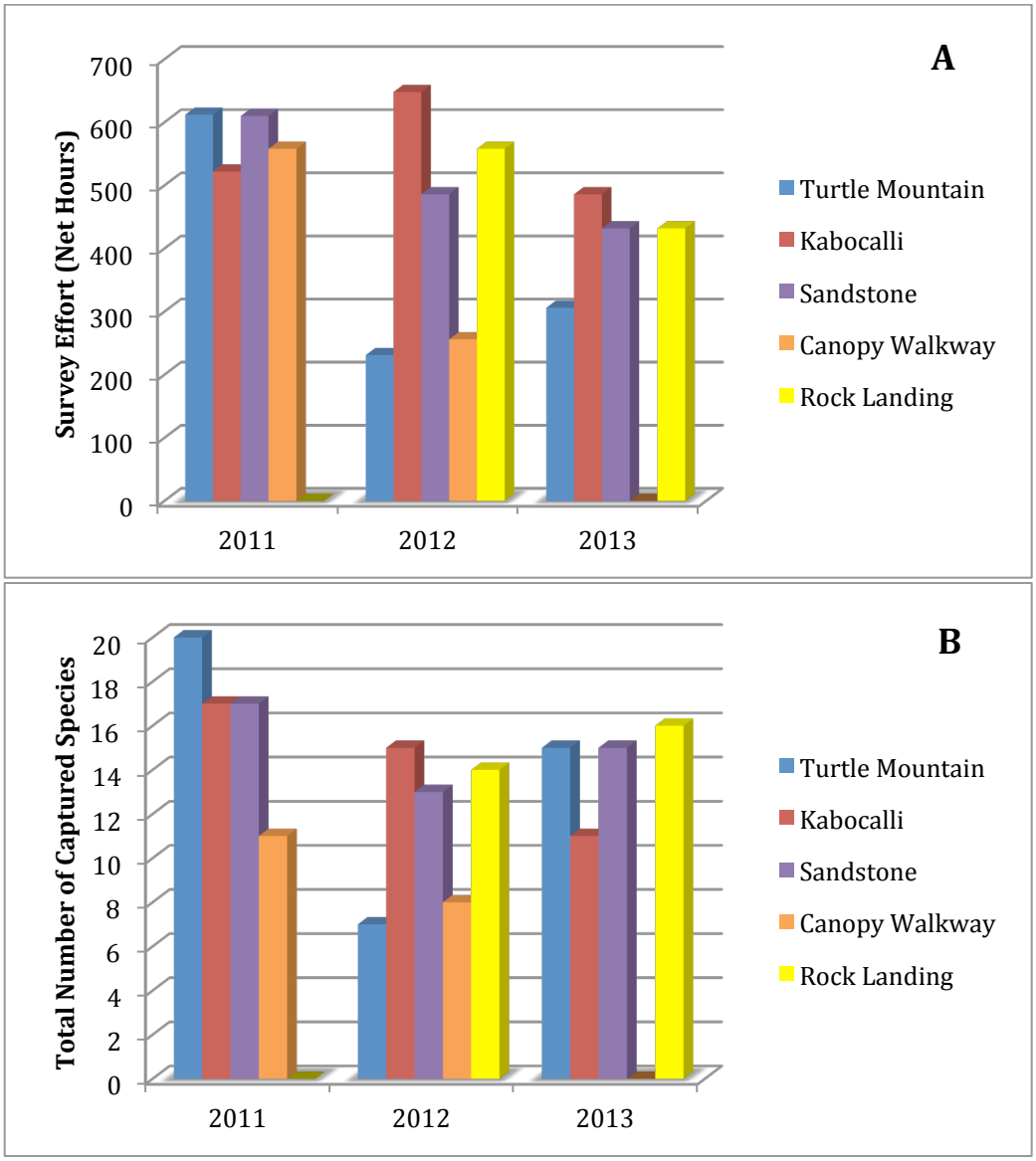

FIGURE 5A. A comparison of the total mist net effort for each site, each year (2011-2013) in the Iwokrama Forest, Guyana from late June to mid August. Survey efforts displayed are the actual survey hours, not including net hours lost due to rainfall. 5B. A comparison of the total number of species captured for each site, each year in Iwokrama Forest, Guyana from late June to mid August.

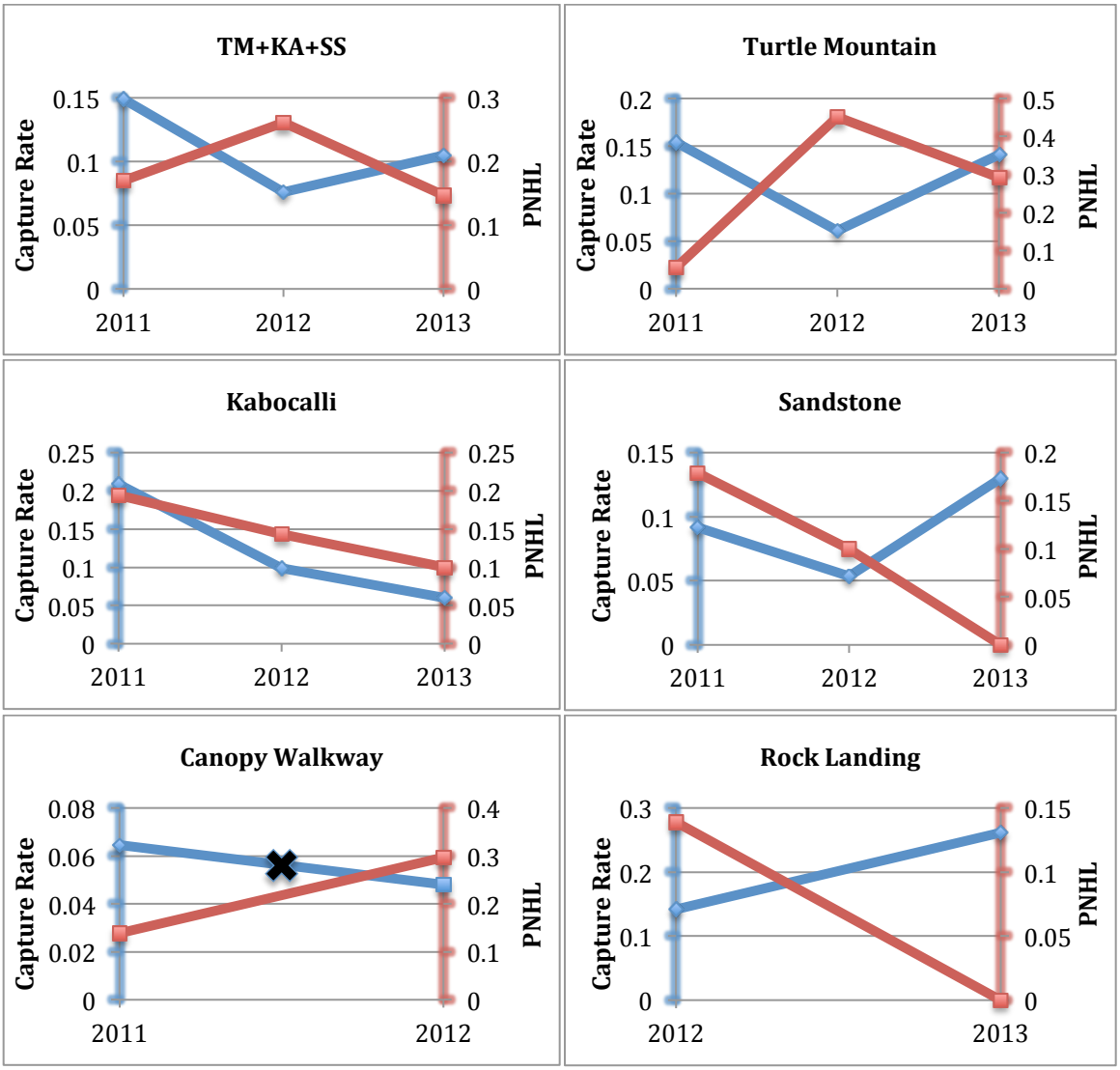

FIGURE 6. A comparison of the combined proportion of net hours lost due to rainfall (red) plotted against the capture rate (Captures/nh) (blue) for the combined Turtle Mountain (TM), Kabocalli (KA), and Sandstone (SS) data, and each site independently. Black "X" over Canopy Walkway capture rates indicates the only non-significant fluctuation between capture rates and PNHL from year to year. All surveys were in the Iwokrama Forest from late June to mid August 2011-2013. These figures illustrate the inverse relationship between the number of hours lost due to rainfall and capture rates of bats at each site. Capture rates shown were calculated using the actual net hours, not including net hours lost due to rainfall.

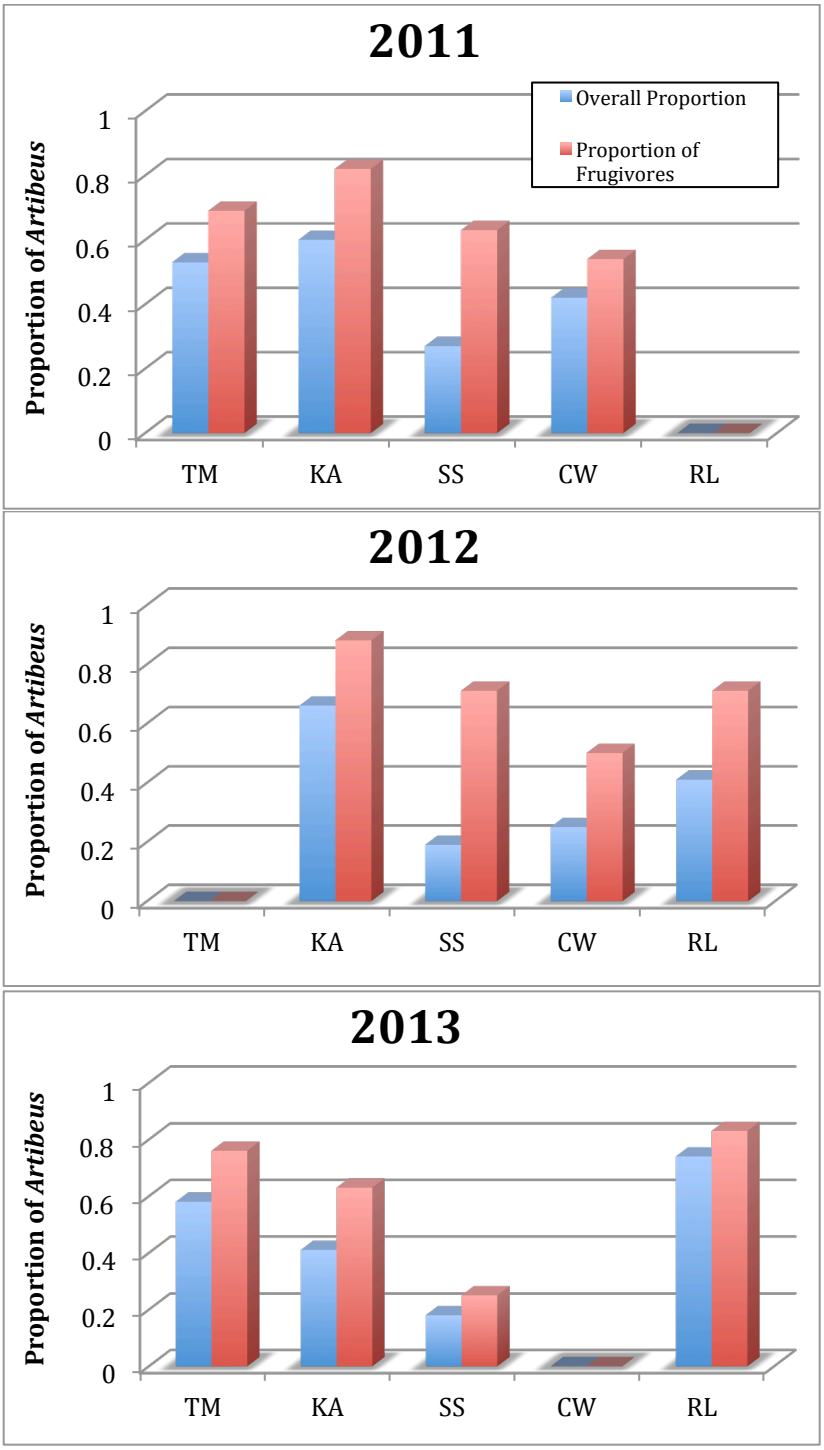

FIGURE 7. Proportion of *Artibeus* (*A. lituratus, A. planirostris,* and *A. obscurus* combined) captured compared to overall captures (blue) and the proportion of *Artibeus* to total captured frugivores (red) for all years (2011-2013) in the Iwokrama Forest, Guyana. Abbreviations: TM – Turtle Mountain, KA – Kabocalli, SS – Sandstone, CW – Canopy Walkway, RL – Rock Landing.

Discussion:

Seed Dispersal

Low sample size and only a single year of surveying limit analysis of dispersal data to two bat genera, *Artibeus* and *Carollia*. Associations between these genera and the plant genera, *Ficus/Cecropia* and *Piper/Solanum,* support the findings of Fleming (1986). *Artibeus* species are considered *Ficus* specialists, and play a critical role in the dispersal of this genus (Morrison 1978a, b; Fleming 1986). In their compilation of known bat dispersal literature, Lobova et al. (2009) found that *Artibeus* accounted for 44% of all records of bat dispersal of *Ficus* species. Furthermore, *Artibeus* species are known as critically important dispersal agents of *Cecropia* species (Lobova et al. 2003). *Carollia* species are considered the primary dispersal agents of *Piper* in the lowland Neotropics (Fleming 2004). Lobova et al. (2009) found that these bats account for 45% of bat dispersal records of *Piper* species. This study found *Artibeus* species accounted for 83% of *Ficus* records and 74% of *Cecropia* records, and *Carollia* species accounted for 75% of *Piper* records and 100% of *Solanum* records.

Additionally, dispersal data support Fleming's (1986) finding that specialization of frugivore diets usually involves a "tradeoff" between quality and quantity of fruit. Bats generally consuming low quality fruit, such as *Artibeus,* tend to specialize on high-density fruits, such as *Ficus*, and bats that tend to seek out high quality fruit, e.g. *Carollia* feeding on *Piper* and *Solanum*, tend to have much broader diets, seeking out many food sources. Overall, in this study *A. lituratus, A. planirostris, and A. obscurus* fed on three plant genera *Ficus, Cecropia,* and *Philodendron*. *Carollia perspicillata* fed on nine genera: *Piper, Solanum, Rollinia, Senna, Anthurium, Paullinia, Philodendron, Vismia,* and *Cecropia*. Minimal dietary overlap occurred between *Artibeus* and *Carollia*, with only two overlapping

plant genera, *Philodendron* and *Cecropia.* Furthermore, each of these plant genera was represented by only a single sample in each group of bats: one *Artibeus* sample contained *Philodendron sp.* and a single *Carollia* sample contained *Cecropia latiloba*. This too is consistent with Fleming's (1988) observations. Identification of *C. latiloba* as a bat dispersed species, in addition to seven new dispersal records of known bat-dispersed plant species being dispersed by novel bat species (Table 2), is reflective of this understudied site. The Iwokrama Forest still holds a wealth of new information to be discovered, moreso than other locations such as Costa Rica and Panama where there have been multiple studies on frugivorous bats (Fleming 1988, Handley et al. 1991).

Cecropia latiloba.

Cecropia latiloba is one of the most efficient colonizers of flood plains throughout its distribution within the Amazon basin and the Guiana Shield (Parolin 2002, Lobova et al. 2003, Zalamea et al. 2011). This efficiency is derived from numerous adaptations for survival in flooded habitat, such as high tolerance to waterlogging and submergence, rapid vertical growth and reiteration capacity, and high tolerance to sediment deposition (Worbes et al. 1992). Its successful establishment leads to monospecific stands and, ultimately, the first closed canopy, which is the initial phase of successional progression leading to very diverse forests (Worbes et al. 1992). The peak flowering and fruiting period of this species is during the wet season, contrary to most other fruit producing plant species over its range (Milton 1991). In the Amazon flood plains, a closely related species, *C. obtusifolia,* flowers during the beginning of the flooded period (February to April), is wind pollinated (Epperson and Alvarez-Buylla 1997), and produces fruit throughout the flooded period (March to July). Fruits of *C. latiloba* mature only at the end of the high water phase, occurring in July and

August, and are adapted for aquatic dispersal by fish (Parolin 2002, Parolin et al. 2010). Fruiting during the height of the rainy season occurs when frugivorous fish species are in their highest densities, thus maximizing dispersal potential (Kubitzki and Ziburski 1994). A single infructescence contains up to 5,000 diaspores, which can survive submersion for up to 2 months (Parolin et al. 2010). However, diaspores exposed to air will dry or decompose within days or weeks. Seeds have high nutrient content, which is advantageous for the seedling, as fast initial growth is guaranteed (Parolin et al. 2010).

Artibeus lituratus, *A. planirostris,* and *A. obscurus* were responsible for six of the nine dispersal records of *Cecropia latiloba*. Foraging on this species is likely not preferential, but opportunistic during times of low availability of their preferred resources. Pericarp of *C. latiloba* infructescences is high in nutrients, thus foraging on this species could prove beneficial for bats during this time (Parolin et al. 2010). However, *C. latiloba* is adapted for ichthyochory, and relies on fish species to carry its diaspores against the current of adjacent rivers, facilitating later germination on freshly deposited sediments (Kubitzki and Ziburski 1994). Furthermore, fish remove the fruit-pulp through partial mastication and gut passage, which breaks seed dormancy, promoting germination (Anderson et al. 2009). Thus, despite potential advantages of consuming *C. latiloba* for the bats, it is likely disadvantageous for this plant. *Artibeus* species do occur near riparian habitat (Handley 1976), so dispersal of *C. latiloba* in an area suitable for its ultimate establishment is possible. This is particularly true of our survey sites in Iwokrama, as they are bordered by large stands of flooded forest, likely favorable for establishment of *C. latiloba.* However, the proportion of bat-consumed diaspores that could ultimately germinate is likely much lower than diaspores consumed by its primary dispersal agent, fish. Moreover, as diaspores of *C. latiloba* will dry or decompose

after prolonged exposure to air, diaspores dispersed by *Artibeus* could easily be deposited in a drier environment, leading to non-viability. Future dietary studies in Guyana could elucidate the frequency of consumption of *C. latiloba* by bats compared to availablility, and potentially determine whether foraging on *C. latiloba* by bats is opportunistic or preferential during the summer wet season.

Cecropia latiloba was found in fecal samples from three of the four surveyed sites. Six dispersal records were recorded from Turtle Mountain, two were from Sandstone, and one was from Rock Landing; no diaspores were collected from Kabocalli. The Turtle Mountain site is located within a large area of flooded forest; this is consistent with the higher abundance of *C. latiloba*. To arrive at this site, one must boat through 400m of flooded forest from the edge of the Essequibo River to the landing. The other sites, including Kabocalli, have substantial flooding of forests on the banks of the Essequibo or Burro-burro Rivers. However, the flooded forest at Turtle Mountain is the most substantial of any site. With additional fecal sample collection, based on site similarity, it is likely that *C. latiloba* will also be found at Kabocalli. Based on the occurrence of *C. latiloba* in fecal samples from the majority of surveyed sites, located throughout Iwokrama, it appears that this species is broadly distributed within flooded forest habitat throughout the reserve.

Surveys of Bat Diversity

The sharp decline in bat captures from 2011 to 2012 is likely due to recognition of nets by previously captured individuals and high rainfall in 2012 (Gannon and Willig 2005). From year to year, rainfall varied in its effect on survey effort among sites. The season in 2012 was the hardest hit with regard to lower bat captures and lower species diversity, followed by 2011 and 2013 (Figure 7). Rainfall affects survey effort in two ways, directly as

a result of net closure and indirectly as fruit production is typically lower during periods of high rainfall, contributing to a reduction of local frugivore abundance due to lower resource availability (Fleming 1986, Milton et al. 2005, Hammond 2005b). This effect was most pronounced during 2012, particularly at Turtle Mountain. Those sites that sustained the highest amount of rainfall in a given season had lower capture rates (Figure 6).

Additionally, previously captured individuals learning to avoid nets and recognizing net locations is a likely contributor to the decline from 2011 (Gannon and Willig 2005). Gardner et al. (1991) noted this effect in their four-year mark/recapture study of *Artibeus jamaicensis* on Barro Colorado Island in Panama. They found that of 8,907 marked individuals captured 15,728 times, 57% were captured only once, 25% were caught twice, and 18% were captured three or more times. Moreover, in a study of *Carollia perspicillata* in Santa Rosa National Park, Costa Rica, Fleming (1988) observed a recapture rate of 14% within the banding year or one year later. Provided that many of the most commonly captured species in Iwokrama have lifespans of at least two years, it is very possible that this phenomenon is affecting Opwall survey results. Little is known about the lifespan of the three focal species of *Artibeus*. However, a closely realted species *A. jamaicensis* is known to have a lifespan of up to nine years in the wild (Gardner et al. 1991). *Carollia perspicillata* is known to have an average life span of 2.6 years, and has been known to reach ages of 10 years in the wild (Fleming 1988).

Interestingly, during Opwall surveys, the number of recaptures from year to year decreased from 20 recaptures in 2011 to six in 2012, to three in 2013. This could possibly indicate increased recognition/avoidance by bats. Marking bats for recapture with a wingpunch serves as an indication of recapture for only a few weeks, as the marking will

heal relatively quickly (Faure et al. 2009). Therefore, this method of marking would not be useful in analyzing recaptures year to year. However, we have noticed bats that bear a circular scar in our standardized wingpunch location (outside of the right leg in the chiropatagium) during surveys in 2012 and 2013. As bats commonly sustain injury to their wings from falls or punctures and bear the scars from those injuries, we cannot be certain that scars on or near our wingpunch location are from a wingpunch applied during prior surveys.

Given the effect of recognition and avoidance of nets, it would appear that data from 2012 and 2013 are more normalized and similar results should be expected for continued years of surveying. Furthermore, the survey results from 2013 provide additional support for this claim, given the only slight resurgence from 2012 when the impact of rainfall on survey effort was significantly reduced from the prior year. If survey results have normalized, one would expect that captured individuals would be primarily adult bats that had not been previously captured and juveniles (Gardner et al. 1991). In future years, banding of captured individuals could shed light on this hypothesis.

Turtle Mountain in 2012 was the only site/season that no individuals of the large *Artibeus*, typically the dominant members of local bat communities, were captured. This is generally a productive site with an average overall capture rate of 0.118 captures/nh; however, during the 2012 season, the PNHL was 0.4514. This represents 195 net hours lost, which accounts for approximately 55% of total net hours lost during that year at all sites. The high rainfall in 2012 contributed heavily to the lower capture rate at this site, as well as the lower capture rate overall for the 2012 season. It also likely contributed to the lack of *Artibeus* captures due to net closure and lower resource availability that is expected during periods of high rainfall (Hammond 2005b, Milton et al. 2005). However, it should be noted

that resource availability was not measured as a part of this study. Additionally, random chance is a likely contributor to the lack of *Artibeus*, as Canopy Walkway in 2012 lost 176 net hours due to rain/fewer nets and three *Artibeus* were still captured.

In 2011, Kabocalli was the most productive site with an overall capture rate of 0.209 captures/nh. However, for each successive year, we witnessed significant declines. *Artibeus* capture rates match the overall pattern for this site. Interestingly, the PNHL actually decreased from year to year, and thus cannot explain the lower capture rates observed. Of all sites surveyed for three years, Kabocalli was the only site to have a significant decrease in capture rate from 2012 to 2013. Sites differ in that Turtle Mountain and Sandstone are located within the sustainable utilization areas of Iwokrama, while Kabocalli is located within the wilderness preserve. Increased disturbance at Turtle Mountain and Sandstone would bring about greater successional heterogeneity surrounding the sites, perhaps contributing to an increase in the variety of fruiting trees and shrubs, contributing to higher frugivore abundance, which could increase capture rates at these sites when compared to Kabocalli (Hammond 2005b). However, given the very high capture rate at Kabocalli in 2011, this would seem unlikely. Additionally, due to a very low number of fecal/stomach content samples collected from this site in 2013, it is difficult to compare dispersed plant species among sites to test this hypothesis. Declining capture rates at Kabocalli could be due to a chance lack of fruiting trees surrounding the site, and/or a greater abundance of fruiting trees in surrounding areas, drawing *Artibeus* away from Kabocalli. This chance proximity of fruiting trees, combined with the flock foraging strategy of large *Artibeus* species (Heithaus et al. 1975), could contribute to very few captures or an abundance of captures of these species, almost a presence/absence scenario. As *Artibeus* species have made up a significant

proportion of total captures at this site (Figure 7), their presence/absence would have a significant effect on the total number of captured individuals.

When considering Sandstone, the observed fluctuation in capture rate from year to year matches the general observed pattern of the combined Turtle Mountain, Kabocalli, and Sandstone data. The PNHL was highest in 2011, and significantly decreased in each successive season (χ^2= 90.7, df= 2, p< 0.001). The significant decrease in capture rate from 2011 to 2012 (χ^2= 16.2, df= 2, p= 0.045), could be attributed to recognition of nets by previously captured individuals, and the significant increase from 2012 to 2013 (χ^2= 16.2, df= 2, p< 0.001) could be due to the significantly lower PNHL (rainfall). The *Artibeus* capture rate was relatively consistent across all years for this site, showing no statistically significant fluctuation. With the exception of Turtle Mountain in 2012, Sandstone had the lowest *Artibeus* capture rates each year. The proportion of the large *Artibeus* species to overall captures/captured frugivores for Sandstone in 2013 is lowest among all sites for all years (Figure 7). This is due to the high number of *Carollia perspicillata* captured, which accounted for over 1/3 of captures for this site in this year.

Fecal sample data collected from Sandstone in 2013, though limited, indicate that consistently low *Artibeus* capture rates could be due to lower availability of their preferred food source, *Ficus*. Sandstone was the only site in which fecal samples collected from *Artibeus* sp. (or other bat species) did not contain *Ficus* diaspores, likely contributing to lower *Artibeus* abundance at this site. This observation can only be considered a hypothesis, as low sample number and only a single year of fecal sample collection preclude statistical analysis and can only be used to draw inferences. Additionally, the higher abundance of *C.*

perspicillata at this site (19 captures in 2013, 0.044 *Carollia* captures/net hour) does correlate with the higher abundance of *Piper* speices identified in fecal samples.

Overall, when compared to other sites, Canopy Walkway had the lowest overall capture rate and, with the exception of Sandstone, the lowest capture rate for *Artibeus* each year. The site was named for the 154 m canopy walkway, which was installed in November of 2003 to promote ecotourism within Iwokrama. In a clearing not far from the walkway, several permanent buildings were constructed to house tourists and researchers, making Canopy Walkway the most developed of any site. However, like Canopy Walkway, Turtle Mountain has several permanent buildings, built for the same purpose, that have been developed in a large clearing. The 18-net survey grids at Turtle Mountain and Canopy Walkway are positioned relatively far from the clearing at each site (TM: 450m and CW: 618m). However, the net grid at Canopy Walkway is positioned within relatively close proximity of the walkway (200m). This positioning was intentional, as surveys of key vertebrate taxa took place prior to the installation of the walkway (dataset not currently published), and Opwall surveys are meant to serve as a means of comparison.

The higher level of development in combination with the proximity of the net grid to the walkway could contribute to the lower capture rates at Canopy Walkway. However, after only two years of surveying and the unavailability of the pre-walkway installation dataset, this observation can only be considered a hypothesis. In addition to being the most developed site, Canopy Walkway is the only site with artificial lighting. Lewanzik and Voigt (2014) have shown that the frugivore *Carollia sowelli* avoided *Piper* infructescences dimly illuminated via artificial light, and preferentially foraged on those infructescences in complete darkness. Thus artificial lighting at the Canopy Walkway site could have

contributed to lower capture rates. Additionally, the PNHL in 2012 for this site was significantly higher than 2011 and only surpassed by Turtle Mountain in the same year(χ^2= 38.9, df= 1, p< 0.001).. Furthermore, during the first of the four nights of surveying at Canopy Walkway in 2012, our group was only able to get 10 of the 18 nets up in the grid due to a later than expected arrival to the site.

In both 2012 and 2013, Rock Landing had the highest capture rate of any site. The *Artibeus* capture rate in 2012 was second only to Kabocalli, and highest among all sites in 2013. According to the 2013 fecal sample data, this site has the highest diversity of plant species collected from the greatest number of diaspore-containing samples, the highest number of *Ficus*-containing samples with the greatest number of *Ficus* species, and was second only to Turtle Mountain in number of samples containing *Cecropia* species. The high overall capture rates for this site could be attributed to the higher plant diversity and the abundance of *Artibeus* is likely reflective of the higher availability of their preferred food sources. Fecal sample data for Turtle Mountain in 2013 also indicate high abundance of *Ficus* and *Cecropia*. However, overall *Artibeus* capture rates are higher at Rock Landing for 2012 and 2013 and could be due to the greater development of Turtle Mountain, as Rock Landing has few semi-permanent buildings within a smaller clearing than Turtle Mountain. From 2012 to 2013 capture rates at Rock Landing significantly increased, presumably due to the significant decrease in PNHL (χ^2= 42.9, df= 1, p< 0.001).

Several studies conducted within the Neotropics have found a similar community composition, biased towards frugivores and specifically *Artibeus* species (Simmons and Voss 1998, Cosson et al. 1999, Simmons et al. 2000, Bernard 2001, Pons and Cosson 2002, Delaval et al. 2005). In their long-term study focusing on *Artibeus jamaicensis* on Barro

Colorado Island, Gardner et al. (1991) found that this single species accounted for an average of 60% of annual captures. In 1979, *A. jamaicensis* was captured 5,484 times out of 9,118 total captures followed by *Artibeus lituratus* (717), *Uroderma bilobatum* (551), and *Carollia perspicillata* (428). Though not as pronounced as Gardner et al. (1991), Fleming (1988) found that *A. jamaicensis* was a significant member of the bat community in Santa Rosa National Park, Costa Rica. Surveys were conducted from 1974-1984, and out of 9,923 total captures, *C. perspicillata* accounted for 59% of captures, followed by *A. jamaicensis* (12%), *Glossophaga soricina* (9%), and *Carollia subrufa* (7%). Furthermore, Gannon and Willig (2005) found *A. jamaicensis* to be one of the dominant species in Puerto Rico during their long-term surveys from 1987 to 1994. These studies were conducted on Central American islands, and as such, these locations would have reduced bat diversity compared to mainland locations due to varying historical dispersal capacities of bats originating from nearby mainland (Ricklefs and Lovette 1999). This needs to be taken into account when comparing results to Opwall surveys. In a short-term, mainland study conducted by Solari et al. (1999) in the Lower Urubamba Region of Peru, *A. lituratus, A. planirostris,* and *A. obscurus* were by far the dominant species, consistent with results of Opwall surveys (this study) in central Guyana.

Most studies examining bat populations in the Neotropics have been short term (1-2 years) (Willig and Moulton 1989, Simmons and Voss 1998, Solari et al. 1999, Bernard 2001), and as such are limited in what they can reveal about community structure, composition, and fluctuation overtime. Few long-term bat-monitoring studies have been conducted to date (Fleming 1988, Gardner et al. 1991), thus continued monitoring at our study site in Guyana is paramount. Jones et al. (2009) argue that bats have tremendous

potential as bioindicators for several reasons: population trends can be monitored, short- and long-term effects on populations can be measured, and bats are broadly distributed. Through the ecosystem services they provide, frugivorous bats reflect the status of local plant species, and insectivorous bat species could reflect changes in the populations of their arthropods prey species. Jones et al. (2009) conclude their argument by saying, "There is an urgent need to implement a global network for monitoring bat populations so their role as bioindicators can be used to its full potential." As Iwokrama is one of the largest reserves in the Guiana shield, containing nearly one million acres of pristine rainforest, it serves as a safe haven for an incredible diversity of species and provides a unique opportunity to monitor an area that could be used as indicator for the overall Guiana Shield. Furthermore, in future surveys, the use of three tier canopy net systems will survey previously untapped strata and likely add additional unrecorded species, further contributing to our understanding of the bat community within the Iwokrama Forest.

Conclusion:

Through seed dispersal, bats provide a critical ecosystem service by assisting with the regeneration of forest habitat (Gardner 1977, Galindo-Gonzalez et al. 2000). As anthropogenic habitat destruction is on the rise in the Neotropics, these bats, and the services they provide, become more and more critical with time (Vitousek et al. 1997). In the present study, 37% of the fecal/stomach content samples from frugivorous bats represented new dispersal records, including a new record of a plant, *Cecropia latiloba*, being bat dispersed (Lobova et al. 2009). Continued dietary research of the bat community within Iwokrama would undoubtedly continue to add to our current understanding of bat/plant interactions as well as the ecological contribution of bats. *Artibeus lituratus, A. planirostris,* and *A. obscurus* play a major ecological role within the Iwokrama forest and across their range. They disperse diaspores of pioneer and early successional plant species, many of which serve as a year round food resource for many other Neotropical species. Based on these characteristics, in addition to their disproportionate abundance and high quality dispersal, I suggest that *Artibeus lituratus, A. planirostris,* and *A. obscurus* should be considered keystone species within the Iwokrama Forest. Research geared toward attaining a better understanding of these species is of the utmost importance to their future conservation, and ultimately the conservation of the community to which they belong.

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APPENDIX 1:

Collected Voucher Specimens- List of all collected voucher specimens of bats from 2012 and 2013 in the Iwokrama Forest, Guyana. All 2012 specimens were deposited in the Royal Ontario Museum in Toronto, Ontario; specimens collected in 2013 were divided between the Royal Ontario Museum and the Angelo State Natural History Collection in San Angelo, Texas. Stomach content samples were collected from specimens marked with an asterisk (*). Additional specimens were collected from a sixth site, the Iwokrama River Lodge (N 4.67153° W-58.68483°).

Species	Locality	Catalog Number	Date Collected
Ametrida centurio	Surama, Rock landing	ROM 122473	1-Aug-13
Artibeus concolor	Iwokrama River Lodge	ROM 122406	18-Jul-13
*Artibeus concolor**	Surama, Rock landing	ASNHC 6481	1-Aug-13
Artibeus gnomus	Iwokrama Forest, Kabocalli	ROM 121978	21-Jul-12
*Artibeus gnomus**	Iwokrama Forest, Kabocalli	ROM 122447	25-Jul-13
Artibeus gnomus	Iwokrama Forest, Kabocalli	ROM 122461	28-Jul-13
*Artibeus lituratus**	Iwokrama Forest, Turtle Mountain	ROM 122417	20-Jul-13
*Artibeus lituratus**	Iwokrama Forest, Turtle Mountain	ROM 122429	21-Jul-13
Artibeus lituratus	Iwokrama Forest, Turtle Mountain	ROM 122436	22-Jul-13
Artibeus lituratus	Iwokrama Forest, Kabocalli	ROM 121984	22-Jul-12
Artibeus lituratus	Iwokrama Forest, Kabocalli	ROM 121990	23-Jul-12
Artibeus lituratus	Iwokrama Forest, Kabocalli	ROM 121997	24-Jul-12
Artibeus lituratus	Iwokrama Forest, Kabocalli	ROM 122001	25-Jul-12
Artibeus lituratus	Iwokrama Forest, Kabocalli	ROM 122005	26-Jul-12
*Artibeus lituratus**	Iwokrama Forest, Kabocalli	ROM 122444	25-Jul-13
*Artibeus lituratus**	Iwokrama Forest, Kabocalli	ROM 122466	29-Jul-13
Artibeus lituratus	Iwokrama Forest, Sandstone	ROM 122062	6-Aug-12
*Artibeus lituratus**	Surama, Rock Landing	ASNHC 16512	1-Aug-13
Artibeus lituratus	Surama, Rock Landing	ASNHC 16513	2-Aug-13
Artibeus lituratus	Surama, Rock Landing	ASNHC 16514	3-Aug-13
Artibeus lituratus	Surama, Rock Landing	ASNHC 16515	4-Aug-13
*Artibeus obscurus**	Iwokrama River Lodge	ROM 121963	18-Jul-12
*Artibeus obscurus**	Iwokrama River Lodge	ROM 121969	19-Jul-12
Artibeus obscurus	Iwokrama River Lodge	ROM 122396	17-Jul-13
Artibeus obscurus	Iwokrama River Lodge	ROM 122405	18-Jul-13
*Artibeus obscurus**	Iwokrama Forest, Turtle Mountain	ROM 122425	21-Jul-13
Artibeus obscurus	Iwokrama Forest, Kabocalli	ROM 121979	21-Jul-12
Artibeus obscurus	Iwokrama Forest, Kabocalli	ROM 121988	22-Jul-12
Artibeus obscurus	Iwokrama Forest, Kabocalli	ROM 121992	23-Jul-12
Artibeus obscurus	Iwokrama Forest, Kabocalli	ROM 121998	24-Jul-12
Artibeus obscurus	Iwokrama Forest, Kabocalli	ROM 121999	25-Jul-12

*Artibeus obscurus**	Iwokrama Forest, Kabocalli	ROM 122446	25-Jul-13
*Artibeus obscurus**	Iwokrama Forest, Kabocalli	ROM 122454	26-Jul-13
*Artibeus obscurus**	Iwokrama Forest, Kabocalli	ROM 122471	29-Jul-13
Artibeus obscurus	Iwokrama Forest, Sandstone	ROM 122051	5-Aug-12
Artibeus obscurus	Iwokrama Forest, Sandstone	ROM 122064	6-Aug-12
Artibeus obscurus	Iwokrama Forest, Sandstone	ROM 122069	10-Aug-12
Artibeus obscurus	Iwokrama Forest, Sandstone	ASNHC 16486	7-Aug-10
Artibeus obscurus	Iwokrama Forest, Sandstone	ASNHC 16520	8-Aug-13
Artibeus obscurus	Surama, Rock Landing	ROM 122017	29-Jul-12
Artibeus obscurus	Surama, Rock Landing	ROM 122020	30-Jul-12
Artibeus obscurus	Surama, Rock Landing	ROM 122028	31-Jul-12
*Artibeus obscurus**	Surama, Rock Landing	ROM 122038	1-Aug-12
*Artibeus obscurus**	Surama, Rock Landing	ROM 122039	2-Aug-12
Artibeus obscurus	Surama, Rock Landing	ASNHC 16516	4-Aug-13
Artibeus obscurus	Surama, Rock Landing	ASNHC 16517	1-Aug-13
Artibeus obscurus	Surama, Rock Landing	ASNHC 16518	2-Aug-13
Artibeus obscurus	Surama, Rock Landing	ASNHC 16519	3-Aug-13
*Artibeus planirostris**	Iwokrama Forest, Turtle Mountain	ROM 122421	20-Jul-13
Artibeus planirostris	Iwokrama Forest, Turtle Mountain	ROM 122430	21-Jul-13
*Artibeus planirostris**	Iwokrama Forest, Turtle Mountain	ROM 122432	22-Jul-13
Artibeus planirostris	Iwokrama Forest, Kabocalli	ROM 121980	21-Jul-12
Artibeus planirostris	Iwokrama Forest, Kabocalli	ROM 121991	23-Jul-12
*Artibeus planirostris**	Iwokrama Forest, Kabocalli	ROM 122000	25-Jul-12
Artibeus planirostris	Iwokrama Forest, Kabocalli	ROM 122006	26-Jul-12
Artibeus planirostris	Iwokrama Forest, Kabocalli	ROM 122445	25-Jul-13
Artibeus planirostris	Iwokrama Forest, Kabocalli	ROM 122462	28-Jul-13
*Artibeus planirostris**	Iwokrama Forest, Kabocalli	ROM 122470	29-Jul-13
Artibeus planirostris	Iwokrama Forest, Sandstone	ROM 122063	6-Aug-12
Artibeus planitrostris	Iwokrama Forest, Sandstone	ASNHC 16485	7-Aug-13
Artibeus planirostris	Surama, Rock Landing	ROM 122016	29-Jul-12
Artibeus planirostris	Surama, Rock Landing	ROM 122019	30-Jul-12
*Artibeus planirostris**	Surama, Rock Landing	ROM 122027	31-Jul-12
Artibeus planirostris	Surama, Rock Landing	ROM 122037	1-Aug-12
Artibeus planirostris	Surama, Rock Landing	ROM 122045	3-Aug-12
Artibeus planirostris	Surama, Rock Landing	ASNHC 16521	1-Aug-13
Artibeus planirostris	Surama, Rock Landing	ASNHC 16522	2-Aug-13
Artibeus planirostris	Surama, Rock Landing	ASNHC 16523	3-Aug-13
*Artibeus planirostris**	Surama, Rock Landing	ASNHC 16524	4-Aug-13
Carollia brevicauda	Iwokrama Forest, Turtle Mountain	ROM 122440	23-Jul-13
*Carollia perspicillata**	Iwokrama River Lodge	ROM 121964	18-Jul-12
*Carollia perspicillata**	Iwokrama River Lodge	ROM 121968	19-Jul-12
Carollia perspicillata	Iwokrama River Lodge	ROM 122397	17-Jul-13

Carollia perspicillata	Iwokrama River Lodge	ROM 122404	18-Jul-13
Carollia perspicillata	Iwokrama Forest, Turtle Mountain	ROM 121967	16-Jul-12
*Carollia perspicillata**	Iwokrama Forest, Turtle Mountain	ROM 122418	20-Jul-13
Carollia perspicillata	Iwokrama Forest, Kabocalli	ROM 121982	21-Jul-12
Carollia perspicillata	Iwokrama Forest, Kabocalli	ROM 122007	26-Jul-12
*Carollia perspicillata**	Iwokrama Forest, Kabocalli	ROM 122458	27-Jul-13
Carollia perspicillata	Iwokrama Forest, Kabocalli	ROM 122464	28-Jul-13
Carollia perspicillata	Iwokrama Forest, Sandstone	ASNHC 16489	7-Aug-13
Carollia perspicillata	Iwokrama Forest, Sandstone	ASNHC 16490	9-Aug-13
Carollia perspicillata	Iwokrama Forest, Sandstone	ASNHC 16491	8-Aug-13
Carollia perspicillata	Iwokrama Forest, Sandstone	ASNHC 16492	6-Aug-13
Carollia perspicillata	Surama, Rock Landing	ASNHC 16493	3-Aug-13
Carollia perspicillata	Surama, Rock Landing	ASNHC 16494	4-Aug-13
Carollia perspicillata	Surama, Rock Landing	ASNHC 16495	1-Aug-13
Carollia perspicillata	Surama, Rock Landing	ASNHC 16496	2-Aug-13
Carollia perspicillata	Surama, Rock Landing	ROM 122013	29-Jul-12
Carollia perspicillata	Surama, Rock Landing	ROM 122021	30-Jul-12
Carollia perspicillata	Surama, Rock Landing	ROM 122026	31-Jul-12
Carollia perspicillata	Surama, Rock Landing	ROM 122036	1-Aug-12
Carollia perspicillata	Surama, Rock Landing	ROM 122044	3-Aug-12
Chiroderma trinitatum	Iwokrama River Lodge	ROM 121975	20-Jul-12
*Chiroderma villosum**	Iwokrama Forest, Sandstone	ROM 122481	6-Aug-13
Chrotopterus auritus	Iwokrama Forest, Kabocalli	ROM 122467	29-Jul-13
Chrotoptorus auritus	Iwokrama Forest, Kabocalli	ROM 121996	24-Jul-12
Chrotoptorus auritus	Iwokrama Forest, Sandstone	ROM 122070	10-Aug-12
Cormura brevirostris	Iwokrama Forest, Sandstone	ROM 122054	5-Aug-12
Cormura brevirostris	Surama, Rock Landing	ROM 122474	1-Aug-13
Desmodus rotundus	Iwokrama Forest, Turtle Mountain	ROM 122415	20-Jul-13
Desmodus rotundas	Iwokrama Forest, Kabocalli	ROM 121981	21-Jul-12
Desmodus rotundas	Iwokrama Forest, Kabocalli	ROM 121989	22-Jul-12
Desmodus rotundas	Iwokrama Forest, Kabocalli	ROM 121994	23-Jul-12
Desmodus rotundus	Iwokrama Forest, Kabocalli	ROM 122459	27-Jul-13
Desmodus rotundus	Surama, Rock Landing	ASNHC 16478	4-Aug-13
Desmodus rotundas	Surama, Rock Landing	ROM 122040	2-Aug-12
Furipterus horrens	Iwokrama Forest, Kabocalli	ROM 122451	26-Jul-13
Glossophaga soricina	Iwokrama River Lodge	ROM 122412	18-Jul-13
Glossophaga soricina	Surama, Rock Landing	ASNHC 16499	1-Aug-13
Glossophaga soricina	Surama, Rock Landing	ROM 122012	29-Jul-12
Glossophaga soricina	Surama, Rock Landing	ROM 122030	31-Jul-12
Glossophaga soricina	Surama, Rock Landing	ROM 122033	31-Jul-12
Glossophaga soricina	Surama, Rock Landing	ROM 122034	1-Aug-12
Glossophaga soricina	Surama, Rock Landing	ROM 122041	2-Aug-12

Glossophaga soricina	Surama, Rock Landing	ROM 122046	3-Aug-12
Glyphonycteris sylvestris	Iwokrama Forest, Kabocalli	ROM 122468	29-Jul-13
Lionycteris spurrelli	Iwokrama Forest, Turtle Mountain	ROM 122434	22-Jul-13
Lionycteris spurrelli	Surama, Rock Landing	ROM 122035	1-Aug-12
Lionycteris spurrelli	Surama, Rock Landing	ROM 122048	3-Aug-12
Lonchophylla thomasi	Iwokrama Forest, Turtle Mountain	ROM 122431	22-Jul-13
Lonchophylla thomasi	Iwokrama Forest, Kabocalli	ROM 122442	25-Jul-13
Lonchophylla thomasi	Iwokrama Forest, Kabocalli	ROM 121976	21-Jul-12
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ASNHC 16487	7-Aug-13
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ASNHC 16501	8-Aug-13
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ASNHC 16502	9-Aug-13
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ROM 122050	5-Aug-12
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ROM 122060	6-Aug-12
Lonchophylla thomasi	Iwokrama Forest, Sandstone	ROM 122065	8-Aug-12
Lonchophylla thomasi	Surama, Rock Landing	ROM 122011	29-Jul-12
Lophostoma schulzi	Iwokrama Forest, Turtle Mountain	ROM 122426	21-Jul-13
Lophostoma schulzi	Surama, Rock Landing	ASNHC 16482	1-Aug-13
Lophostoma silvicolum	Iwokrama River Lodge	ROM 122407	18-Jul-13
Lophostoma silvicolum	Iwokrama Forest, Turtle Mountain	ROM 122438	22-Jul-13
Lophostoma silvicolum	Iwokrama Forest, Kabocalli	ROM 121993	23-Jul-12
Lophostoma silvicolum	Iwokrama Forest, Kabocalli	ROM 121995	24-Jul-12
Lophostoma silvicolum	Iwokrama Forest, Kabocalli	ROM 122003	25-Jul-12
Lophostoma silvicolum	Iwokrama Forest, Sandstone	ROM 122056	5-Aug-12
Lophostoma silvicolum	Iwokrama Forest, Sandstone	ROM 122058	5-Aug-12
Lophostoma silvicolum	Iwokrama Forest, Sandstone	ROM 122066	8-Aug-12
Lophostoma silvicolum	Iwokrama Forest, Sandstone	ASNHC 16509	7-Aug-13
Lophostoma silvicolum	Surama, Rock Landing	ASNHC 16510	2-Aug-13
Lophostoma silvicolum	Surama, Rock Landing	ASNHC 16511	1-Aug-13
Lophostoma silvicolum	Surama, Rock Landing	ROM 122014	29-Jul-12
Lophostoma silvicolum	Surama, Rock Landing	ROM 122022	30-Jul-12
Lophostoma silvicolum	Surama, Rock Landing	ROM 122031	31-Jul-12
Lophostoma silvicolum	Surama, Rock Landing	ROM 122042	2-Aug-12
Lophostoma silvicolum	Surama, Rock Landing	ROM 122047	3-Aug-12
Mesophylla macconnelli	Surama, Rock Landing	ROM 122025	30-Jul-12
*Mesophylla macconnelli**	Surama, Rock Landing	ROM 122480	4-Aug-13
Micoureus demerarae	Surama, Rock Landing	ROM 122049	3-Aug-12
Micronycteris megalotis	Iwokrama Forest, Kabocalli	ROM 122450	26-Jul-13
Micronycteris megalotis	Iwokrama Forest, Kabocalli	ROM 121977	21-Jul-12
Micronycteris megalotis	Iwokrama Forest, Sandstone	ROM 122071	10-Aug-12
Micronycteris megalotis	Iwokrama Forest, Sandstone	ROM 122072	10-Aug-12
Micronycteris minuta	Iwokrama River Lodge	ROM 122400	17-Jul-13

Micronycteris minuta	Iwokrama River Lodge	ROM 122403	18-Jul-13
Mimon bennettii	Iwokrama Forest, Turtle Mountain	ROM 122435	22-Jul-13
Mimon crenulatum	Iwokrama River Lodge	ROM 122399	17-Jul-13
Mimon crenulatum	Iwokrama River Lodge	ROM 122410	18-Jul-13
Mimon crenulatum	Iwokrama River Lodge	ROM 121970	19-Jul-12
Mimon crenulatum	Iwokrama Forest, Kabocalli	ROM 121987	22-Jul-12
Mimon crenulatum	Iwokrama Forest, Sandstone	ROM 122053	5-Aug-12
Mimon crenulatum	Surama, Rock Landing	ASNHC 16480	4-Aug-13
Molossus molossus	Iwokrama River Lodge	ROM 121974	20-Jul-12
Molossus molossus	Iwokrama River Lodge	ROM 122401	17-Jul-13
Molossus molossus	Iwokrama Forest, Turtle Mountain	ROM 122422	20-Jul-13
Molossus molossus	Iwokrama Forest, Turtle Mountain	ROM 122427	21-Jul-13
Molossus molossus	Iwokrama Forest, Turtle Mountain	ROM 122433	22-Jul-13
Molossus molossus	Iwokrama Forest, Turtle Mountain	ROM 122441	23-Jul-13
Molossus molossus	Iwokrama Forest, Kabocalli	ROM 122010	28-Jul-12
Myotis riparius	Iwokrama River Lodge	ROM 122408	18-Jul-13
Myotis riparius	Surama, Rock Landing	ASNHC 16484	2-Aug-13
Noctilio albiventris	Iwokrama River Lodge	ROM 122402	17-Jul-13
Noctilio albiventris	Iwokrama River Lodge	ROM 122409	18-Jul-13
Noctilio leporinus	Surama, Rock Landing	ROM 122477	2-Aug-13
Phylloderma stenops	Surama, Rock Landing	ROM 122024	30-Jul-12
Phylloderma stenops	Surama, Rock Landing	ROM 122032	31-Jul-12
Phyllostomus discolor	Iwokrama Forest, Kabocalli	ROM 122472	29-Jul-13
Phyllostomus elongatus	Iwokrama Forest, Turtle Mountain	ROM 122420	20-Jul-13
Phyllostomus elongatus	Iwokrama Forest, Kabocalli	ROM 122004	25-Jul-12
Phyllostomus elongatus	Iwokrama Forest, Kabocalli	ROM 122443	25-Jul-13
Phyllostomus elongatus	Iwokrama Forest, Kabocalli	ROM 122456	27-Jul-13
Phyllostomus elongatus	Iwokrama Forest, Sandstone	ROM 122052	5-Aug-12
Phyllostomus elongatus	Iwokrama Forest, Sandstone	ROM 122059	6-Aug-12
Phyllostomus elongatus	Iwokrama Forest, Sandstone	ROM 122073	10-Aug-12
Phyllostomus elongatus	Iwokrama Forest, Sandstone	ASNHC 16505	7-Aug-13
Phyllostomus elongatus	Surama, Rock Landing	ASNHC 16506	1-Aug-13
Phyllostomus elongatus	Surama, Rock Landing	ROM 122015	29-Jul-12
Phyllostomus elongatus	Surama, Rock Landing	ROM 122043	2-Aug-12
Phyllostomus hastatus	Surama, Rock Landing	ROM 122478	2-Aug-13
Phyllostomus hastatus	Surama, Rock Landing	ASNHC 16483	3-Aug-13
*Platyrrhinus helleri**	Iwokrama Forest, Turtle Mountain	ROM 122423	20-Jul-13
Platyrrhinus helleri	Surama, Rock Landing	ROM 122029	31-Jul-12
Pteronotus parnellii	Iwokrama River Lodge	ROM 122414	18-Jul-13
Pteronotus parnellii	Iwokrama River Lodge	ROM 121965	18-Jul-12
Pteronotus parnellii	Iwokrama Forest, Turtle Mountain	ROM 122419	20-Jul-13
Pteronotus parnellii	Iwokrama Forest, Turtle Mountain	ROM 122428	21-Jul-13

Pteronotus parnellii	Iwokrama Forest, Kabocalli	ROM 121986	22-Jul-12
Pteronotus parnellii	Iwokrama Forest, Kabocalli	ROM 122448	25-Jul-13
Pteronotus parnellii	Iwokrama Forest, Kabocalli	ROM 122452	26-Jul-13
Pteronotus parnellii	Iwokrama Forest, Kabocalli	ROM 122455	27-Jul-13
Pteronotus parnelli	Iwokrama Forest, Sandstone	ASNHC 16488	7-Aug-13
Pteronotus parnellii	Iwokrama Forest, Sandstone	ROM 122055	5-Aug-12
Pteronotus parnellii	Iwokrama Forest, Sandstone	ROM 122068	10-Aug-12
Pteronotus parnellii	Surama, Rock Landing	ROM 122018	30-Jul-12
Pteronotus parnelli	Surama, Rock Landing	ASNHC 16527	3-Aug-13
Pteronotus parnelli	Surama, Rock Landing	ASNHC 16528	2-Aug-13
Pteronotus personatus	Surama, Rock Landing	ROM 122479	3-Aug-13
Rhynchonycteris naso	Iwokrama River Lodge	ROM 121972	19-Jul-12
Rhynchonycteris naso	Iwokrama River Lodge	ROM 122398	17-Jul-13
Rhynchonycteris naso	Surama, Rock Landing	ASNHC 16500	3-Aug-13
*Rhinophylla pumilio**	Iwokrama Forest, Turtle Mountain	ROM 122416	20-Jul-13
Rhinophylla pumilio	Iwokrama Forest, Kabocalli	ROM 121983	21-Jul-12
Rhinophylla pumilio	Iwokrama Forest, Kabocalli	ROM 122002	25-Jul-12
*Rhinophylla pumilio**	Iwokrama Forest, Kabocalli	ROM 122449	26-Jul-13
*Rhinophylla pumilio**	Iwokrama Forest, Kabocalli	ROM 122469	29-Jul-13
*Rhinophylla pumilio**	Iwokrama Forest, Sandstone	ASNHC 16525	9-Aug-13
Rhinophylla pumilio	Iwokrama Forest, Sandstone	ASNHC 16526	8-Aug-13
Saccopteryx bilineata	Iwokrama River Lodge	ROM 122413	18-Jul-13
Saccopteryx bilineata	Iwokrama River Lodge	ROM 121966	18-Jul-12
Saccopteryx bilineata	Iwokrama River Lodge	ROM 121971	19-Jul-12
Saccopteryx bilineata	Iwokrama River Lodge	ROM 121973	20-Jul-12
Saccopteryx bilineata	Iwokrama Forest, Sandstone	ROM 122061	6-Aug-12
Saccopteryx bilineata	Surama, Rock Landing	ASNHC 16497	1-Aug-13
Saccopteryx bilineata	Surama, Rock Landing	ASNHC 16498	4-Aug-13
*Sturnira lilium**	Surama, Rock Landing	ROM 122475	1-Aug-13
Sturnira tildae	Iwokrama Forest, Sandstone	ASNHC 16503	9-Aug-13
Sturnira tildae	Iwokrama Forest, Sandstone	ASNHC 16504	7-Aug-13
Sturnira tildae	Iwokrama Forest, Sandstone	ROM 122482	8-Aug-13
*Sturnira tildae**	Surama, Rock Landing	ROM 122476	2-Aug-13
*Sturnira tildae**	Surama, Rock Landing	ASNHC 16479	4-Aug-13
Thyroptera tricolor	Iwokrama Forest, Turtle Mountain	ROM 122439	22-Jul-13
Thyroptera tricolor	Iwokrama Forest, Kabocalli	ROM 122008	28-Jul-12
Thyroptera tricolor	Iwokrama Forest, Kabocalli	ROM 122009	28-Jul-12
Tonatia saurophila	Surama, Rock Landing	ROM 122023	30-Jul-12
Trachops cirrhosus	Iwokrama River Lodge	ROM 122411	18-Jul-13
Trachops cirrhosus	Iwokrama Forest, Kabocalli	ROM 121985	22-Jul-12
Trachops cirrhosus	Iwokrama Forest, Kabocalli	ROM 122453	26-Jul-13
Trachops cirrhosus	Iwokrama Forest, Kabocalli	ROM 122457	27-Jul-13

Trachops cirrhosus	Iwokrama Forest, Sandstone	ROM 122057	5-Aug-12
*Vampyressa bidens**	Iwokrama Forest, Turtle Mountain	ROM 122424	20-Jul-13
Vampyressa bidens	Iwokrama Forest, Turtle Mountain	ROM 122437	22-Jul-13
*Vampyressa bidens**	Iwokrama Forest, Kabocalli	ROM 122463	28-Jul-13
*Vampyressa bidens**	Iwokrama Forest, Sandstone	ASNHC 16508	9-Aug-13
*Vampyressa bidens**	Surama, Rock Landing	ASNHC 16507	1-Aug-13

APPENDIX 2:

Captured Individuals Inventory- Capture data including the number of each species captured each year for the combined Turtle Mountain, Kabocalli, and Sandstone dataset, and each site individually from the Iwokrama Forest, Guyana.

Capture data from the Combined Turtle Mountain, Kabocalli, and Sandstone dataset.

Captured Species	**2011**	**2012**	**2013**
Artibeus concolor	1	0	0
Artibeus gnomus	0	2	2
Artibeus lituratus	35	15	15
Artibeus obscurus	22	21	13
Artibeus planirostris	73	11	19
Carollia brevicauda	0	0	1
Carollia perspicillata	22	7	21
Chiroderma villosum	3	0	1
Chrotopterus auritus	1	2	0
Cormura brevirostris	0	1	0
Desmodus rotundus	6	4	3
Furipterus horrens	1	0	1
Glossophaga soricina	4	1	1
Lionycteris spurrelli	0	0	2
Lonchophylla thomasi	10	7	6
Lophostoma brasiliense	1	0	0
Lophostoma schulzi	1	1	1
Lophostoma silvicolum	25	10	3
Mesophylla macconnelli	1	0	0
Micronycteris brachyotis	1	0	0
Micronycteris megalotis	3	2	0
Micronycteris minuta	1	0	0
Mimon bennettii	1	0	1
Mimon crenulatum	4	2	0
Phylloderma stenops	2	0	0
Phyllostomus elongatus	11	3	5
Platyrrhinus helleri	1	0	0
Pteronotus parnellii	8	8	9
Rhinophylla pumilio	7	3	15
Saccopteryx bilineata	0	1	0
Sturnira tildae	0	0	5
Thyroptera tricolor	0	0	1
Tonatia saurophila	2	1	0

Trachops cirrhosus	5	2	2
Uroderma bilobatum	2	0	0
Vampyressa bidens	4	0	1
Vampyrum spectrum	1	0	0
Total Captures:	**259**	**104**	**128**
Number of Species:	**30**	**20**	**22**
Capture Rate:	**0.169**	**0.076**	**0.105**

Capture data from Turtle Mountain.

Captured Species	**2011**	**2012**	**2013**
Artibeus concolor	1	0	0
Artibeus lituratus	12	0	12
Artibeus obscurus	7	0	1
Artibeus planirostris	31	0	12
Carollia brevicauda	0	0	1
Carollia perspicillata	8	6	2
Chiroderma villosum	3	0	0
Desmodus rotundus	1	1	1
Glossophaga soricina	2	1	0
Lionycteris spurrelli	0	0	2
Lonchophylla thomasi	4	0	0
Lophastoma schulzi	0	1	1
Lophostoma brasiliense	1	0	0
Lophostoma silvicolum	6	0	1
Micronycteris megalotis	2	0	0
Mimon bennettii	1	0	1
Phylloderma stenops	1	0	0
Phyllostomus elongatus	4	0	1
Pteronotus parnellii	2	3	3
Rhinophylla pumilio	1	1	3
Thyroptera tricolor	0	0	1
Tonatia saurophila	2	1	0
Trachops cirrhosus	3	0	0
Vampyressa bidens	0	0	1
Uroderma bilobatum	2	0	0
Total Captures:	**94**	**14**	**43**
Number of Species:	**20**	**7**	**15**
Capture Rate:	**0.154**	**0.061**	**0.141**

Capture data from Kabocalli.

Captured Species	**2011**	**2012**	**2013**
Artibeus gnomus	0	2	1
Artibeus lituratus	21	14	2
Artibeus obscurus	10	18	5
Artibeus planirostris	34	10	5
Carollia perspicillata	4	1	0
Chrotopterus auritus	1	1	0
Desmodus rotundus	5	3	1
Furipterus horrens	0	0	1
Glossophaga soricina	1	0	0
Lonchophylla thomasi	3	3	2
Lophostoma silvicolum	14	4	0
Micronycteris megalotis	1	1	0
Micronycteris minuta	1	0	0
Mimon crenulatum	1	1	0
Phyllostomus elongatus	3	1	2
Pteronotus parnellii	0	2	5
Rhinophylla pumilio	3	2	4
Trachops cirrhosus	2	1	1
Vampyressa bidens	4	0	0
Vampyrum spectrum	1	0	0
Total Captures:	**109**	**64**	**29**
Number of Species:	**17**	**15**	**11**
Capture Rate:	**0.209**	**0.099**	**0.06**

Capture Data from Sandstone.

Captured Species	**2011**	**2012**	**2013**
Artibeus gnomus	0	0	1
Artibeus lituratus	2	1	1
Artibeus obscurus	5	3	7
Artibeus planirostris	8	1	2
Carollia perspicillata	10	0	19
Chiroderma villosum	0	0	1
Chrotopterus auritus	0	1	0
Cormura brevirostris	0	1	0
Desmodus rotundus	0	0	1
Furipterus horrens	1	0	0
Glossophaga soricina	1	0	1
Lonchophylla thomasi	3	4	4

Lophostoma schulzi	1	0	0
Lophostoma silvicolum	5	6	2
Mesophylla macconnelli	1	0	0
Micronycteris brachyotis	1	0	0
Micronycteris megalotis	0	1	0
Mimon crenulatum	3	1	0
Phylloderma stenops	1	0	0
Phyllostomus elongatus	4	2	2
Platyrrhinus helleri	1	0	0
Pteronotus parnellii	6	3	1
Rhinophylla pumilio	3	0	8
Saccopteryx bilineata	0	1	0
Sturnira tildae	0	0	5
Trachops cirrhosus	0	1	1
Total Captures:	**56**	**26**	**56**
Number of Species:	**17**	**13**	**15**
Capture Rate:	**0.092**	**0.053**	**0.129**

Capture data from Canopy Walkway.

Captured Species	**2011**	**2012**
Artibeus lituratus	5	0
Artibeus obscurus	2	2
Artibeus planirostris	8	1
Carollia perspicillata	7	2
Chrotopterus auritus	0	1
Glossophaga soricina	2	3
Lophostoma silvicolum	1	0
Mimon bennettii	2	0
Phyllostomus elongatus	1	0
Pteronotus parnellii	3	0
Rhinophylla pumilio	4	1
Tonatia saurophila	0	1
Trachops cirrhosus	0	1
Vampyressa bidens	1	0
Total Captures:	**36**	**12**
Number of Species:	**11**	**8**
Capture Rate:	**0.065**	**0.047**

Capture data from Rock Landing.

Captured Species	**2012**	**2013**
Artibeus concolor	0	1
Artibeus lituratus	0	15
Artibeus obscurus	9	18
Artibeus planirostris	23	51
Carollia perspicillata	9	10
Desmodus rotundus	1	2
Glossophaga soricina	6	1
Lionycteris spurrelli	3	0
Lonchophylla thomasi	4	0
Lophastoma schulzi	0	1
Lophostoma silvicolum	13	6
Mesophylla macconnelli	1	1
Mimon crenulatum	0	1
Phylloderma stenops	2	0
Phyllostomus elongatus	2	2
Platyrrhinus helleri	1	0
Pteronotus parnellii	4	1
Tonatia saurophila	1	0
Sturnira lilium	0	1
Sturnira tildae	0	1
Vampyressa bidens	0	1
Total Captures	**79**	**113**
Number of Species:	**14**	**16**
Capture Rate:	**0.142**	**0.262**

APPENDIX 3.

Dispersed Plant Species Inventory- List detailing the 20 dispersed plant species identified in fecal and stomach content samples collected in 2013 from study sites within the Iwokrama Forest, Guyana. Along with plant species, the number of samples in which each plant species occurred and bat genera whose samples contained each plant species are displayed.

Plant Species	**Sample #**	**Bat Species (# of Samples)**
Ficus nymphaeifolia	12	*A. lituratus* (2), *A. obscurus*, *A. planirostris* (7), *V. bidens* (2)
Piper bartlingianum	12	*C. perspicillata* (8), *R. pumilio*, *S. tildae* (3)
Cecropia latiloba	9	*A. lituratus, A. obscurus* (2), *A. planirostris* (3), *C. perspicillata*, *P. helleri, V. bidens*
Cecropia sciadophylla	8	*A. lituratus* (4), *A. obscurus, A. planirostris, P. hastatus, S. lilium*
Solanum rugosum	5	*C. perspicillata* (5)
Ficus panurensis	4	*A. gnomus, A. planirostris* (3)
Rollinia exsucca	4	*C. perspicillata* (4)
Piper trichoneuron	2	*C. perspicillata*
Senna quinquangulata	2	*C. perspicillata* (2)
Anthurium trinerve	1	*C. perspicillata*
Cecropia obtusa	1	*A. obscurus*
Cecropia sp.	1	*A. lituratus*
Ficus insipida	1	*A. planirostris*
Ficus maxima	1	*A. obscurus*
Paullinia sp.	1	*C. perspicillata*
Philodendron guianense	1	*C. perspicillata*
Philodendron sp.	1	*A. lituratus*
Piper anonifolium	1	*C. perspicillata*
Piper hostmannianum	1	*C. perspicillata*
Vismia cayennensis	1	*C. perspicillata*